



A Spark in the Dark: Uncovering Natural Activity Patterns of Mormyrid Weakly Electric Fish

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To understand animal ecology, observation of wildlife in the natural habitat is essential, but particularly challenging in the underwater realm. Weakly electric fishes provide an excellent opportunity to overcome some of these challenges because they generate electric organ discharges (EODs) to sense their environment and to communicate, which can be detected non-invasively. We tracked the EOD and swimming activity of two species of mormyrid weakly electric fishes (*Marcusenius victoriae* and *Petrocephalus degeni*) over diel cycles in the laboratory, and we recorded EODs and environmental dissolved oxygen (DO) concentration and temperature over several months in a naturally hypoxic habitat in Uganda. Under laboratory conditions, both species showed increases of activity and exploration behavior that were closely synchronized to the onset of the dark phase. In the wild, fish preferred structurally complex habitats during the day, but dispersed toward open areas at night, presumably to forage and interact. Nocturnal increase of movement range coincided with diel declines in DO concentration to extremely low levels. The fact that fish showed pronounced nocturnal activity patterns in the laboratory and in the open areas of their habitat, but not under floating vegetation, indicates that light intensity exerts a direct effect on their activity. We hypothesize that being dark-active and tolerant to hypoxia increases the resistance of these fish against predators. This study establishes a new technology to record EODs in the field and provides a window into the largely unknown behavior of mormyrids in their natural habitat.

Keywords: behavioral activity, habitat use, electric organ discharge, hypoxia, swim behavior

INTRODUCTION

From the morning songs of birds to the seasonal migrations of salmon, rhythmic patterns of behavior are ubiquitous in nature across all taxa of animals (Wulund and Reddy, 2015; Häfker and Tessmar-Raible, 2020). Rhythmic behavior is driven by cyclical (abiotic) shifts in environmental conditions, such as the day/night cycle, the lunar cycle, and seasonal changes, e.g., in temperature and rainfall. The predictable nature of these cycles has made it possible for organisms to adapt to, and anticipate, environmental change in order to optimize the use of resources and environmental conditions (Häfker and Tessmar-Raible, 2020).

Many aquatic habitats are characterized by rhythmic changes in environmental conditions, although these may differ from terrestrial cycles. Light and temperature, reliable terrestrial diel time cues (Hut et al., 2013), can be less predictable underwater. In deep and/or turbid water bodies, ambient light levels may reach values where day and night are indistinguishable. The large heat capacity of water and other factors, such as rainfall or vertical mixing, can affect daily temperature cycles (Hut et al., 2013; Häfker and Tessmar-Raible, 2020). Fluctuations of dissolved oxygen (DO) concentration on the other hand, are mostly negligible on land but can be subject to pronounced rhythms in water bodies. Reduced input of photosynthetically produced oxygen during the night affects diel shifts in DO concentration. Seasonal effects, such as ice cover and rainfall can shift DO concentration over a longer timescale (e.g., Greenbank, 1945; Talling, 1957; Kannan and Job, 1980; Townsend, 1999). Alongside DO levels, pH and CO₂ concentration can fluctuate substantially on a diel and seasonal timescale (Semesi et al., 2009; Baumann et al., 2015). In tropical ecosystems, increased rainfall during the wet season can change inundation levels, flush nutrients and pollutants into water bodies and thereby change their hydrochemistry drastically (Adebisi, 1981; Hamilton, 2010).

Adaptive behavioral rhythms are just as commonly found in marine and freshwater habitats as on land (Naylor, 2010; Häfker and Tessmar-Raible, 2020). Among these, rhythms that occur on a diel timescale have been studied most intensively. Many aspects of fish behavior follow such diel rhythms, for example, shelter use (Vanderpham et al., 2012), swimming activity (Tabata et al., 1989; Hurd et al., 1998), food intake (Boujard and Leatherland, 1992; Sánchez-Vázquez et al., 1995), foraging behavior and migration (Hobson, 1973; Neilson and Perry, 1990; Ibbotson et al., 2006), and the formation of fish assemblages (Rooker and Dennis, 1991; Arrington and Winemiller, 2003). On a longer timescale, migration and reproductive behavior have been found in many species to be linked to lunar, seasonal, and annual rhythms (reviewed in Volpato and Trajano, 2005).

The study of activity rhythms in the field is challenging, and this is particularly true for the study of aquatic animals, mostly due to the logistical challenges and limitations of underwater sampling methods that are associated with them. For example, most studies on fish activity rhythms that are carried out in tropical regions are based on direct observation (Volpato and Trajano, 2005; Frehse et al., 2020, 2021). These studies are subject to a sampling bias that favors species that are diurnal and live in clear water. Hence, natural behavioral patterns of more elusive fish species, such as nocturnal fishes, remain largely unknown. In this respect, weakly electric fishes offer unique opportunities for behavioral observations in their natural habitat. They generate an electric field around their body by emitting species-specific electric organ discharges (EODs, Lissmann, 1951), which they use to navigate and forage (Lissmann, 1958; Lissmann and Machin, 1958), and to communicate with conspecifics (Moller, 1970; Moller and Bauer, 1973; Carlson, 2002). By recording their EODs with electrodes, the presence, activity state, number, and (if the EOD waveform is known) species of weakly electric fish can be detected in a water body without the need for visual or acoustic sampling (e.g., Lissmann and Schwassmann, 1965;

Henninger et al., 2018, 2020; Madhav et al., 2018; Migliaro et al., 2018).

Weakly electric fishes are widespread in tropical freshwater habitats in Central and South America and throughout Africa where they constitute important food web components (Lundberg et al., 1987; Moller, 1995; Crampton, 1996). They are generally considered nocturnal animals, and this has been documented in some species that show nocturnal increases of locomotor and EOD activity in the laboratory (Harder et al., 1964; Bässler et al., 1979; Cobert, 1984; Franchina and Stoddard, 1998; Markham et al., 2009; Migliaro and Silva, 2016). Field studies generally support the notion of nocturnality in weakly electric fishes (Lissmann, 1961; Lissmann and Schwassmann, 1965; Kruger, 1973; Moller et al., 1979; Henninger et al., 2018, 2020; Madhav et al., 2018; Migliaro et al., 2018). However, a close examination of this body of research shows that there are examples of weakly electric fish that remain active during the day (e.g., in dark habitats, Kruger, 1973; Hopkins, 1980), and that nocturnal activity patterns have often been observed in shallow and/or clear water habitats, where light conditions change drastically from day to night (Lissmann, 1961; Lissmann and Schwassmann, 1965; Henninger et al., 2018, 2020). Thus, it seems that the activity of weakly electric fishes in the wild corresponds more closely to ambient light levels than to the phase of the diel cycle. It is therefore likely that activity patterns of many of the >450 species of weakly electric fishes (Crampton, 2019) depend on light conditions among other exogenous and endogenous factors, and that these animals might not always classify as nocturnal. Previous studies have shown that fishes can display extraordinary plasticity in their diel and circadian activity rhythms (reviewed in Reeb, 2002). Other factors than illumination, such as social stimuli (Franchina et al., 2001; Silva et al., 2007) and temperature (Dunlap et al., 2000; Ardanaz et al., 2001), can affect activity, and the interplay of these and other, hitherto unknown environmental influences, might shape natural behavioral patterns that differ from those observed in the laboratory. An environmental factor whose influence on diel behavior has been studied little in the field is ambient DO (Pollock et al., 2007). Many weakly electric fishes experience seasonal, diel, or chronic hypoxia (Chapman et al., 1996b; Crampton, 1998). Usually, DO reaches the lowest levels during the night due to respiration and lack of photosynthesis. The degree to which weakly electric fish can tolerate hypoxia might be limited by the energetic costs for generation and sensing of EODs (Salazar and Stoddard, 2008; Salazar et al., 2013; Lewis et al., 2014; Sukhum et al., 2016). With the large ionic currents underlying EOD generation (Markham et al., 2009), electric organs are considered to be energetically similarly expensive tissue as brains, but make up a larger proportion of body mass than brain tissue (Markham et al., 2016). Little is known about how environmental rhythms, such as diel patterns of hypoxia, affect the activity of weakly electric fish, and how representative laboratory studies are of natural activity patterns of fish.

The aim of this study was to investigate and compare activity and habitat use of mormyrid weakly electric fish in the laboratory and in the wild. *Marcusenius victoriae* and *Petrocephalus degeni*

occur in a severely hypoxic swamp habitat in Uganda and show a high degree of hypoxia tolerance (Chapman and Chapman, 1998; Clarke et al., 2020; Moulton et al., 2020). They belong to different subfamilies of the Mormyridae, Mormyrinae and Petrocephalinae, respectively, and differ in their electrosensory anatomy, overall morphology, and social behavior (Carlson, 2016). *Marcusenius victoriae* are medium sized fish (usually 7–15 cm standard length) that are found predominantly alone in nature and show a high degree of intraspecific competition for shelters (Carlson, 2016). *Petrocephalus degeni* are shorter fish (usually 5–9 cm standard length) that are often found in groups and show pronounced social affiliation behavior (Carlson, 2016). Both species produce very short (ca. 300–500 μ s), bi- or triphasic EOD pulses with a species-specific waveform (**Supplementary Figure 1A**). The diel variation of DO in their swamp habitat has not been quantified yet, and no detailed description of their diel habitat use and activity rhythms exists.

We conducted laboratory and field work to assess behavioral patterns under controlled and natural conditions. We captured fish from their swamp habitat and acclimated them to standardized laboratory housing conditions for one year before measuring diel patterns of EOD and locomotor activity in a 12:12 h light:dark environment under constant temperature and DO. To assess the behavioral patterns of *M. victoriae* and *P. degeni* in their habitat, we developed and built autonomous EOD recording devices. We measured the diel cycling of environmental temperature and DO, and recorded EODs in three habitats within a swamp lagoon system between July and September 2019 to document diel patterns of activity and habitat use, and abiotic environmental cycles.

MATERIALS AND METHODS

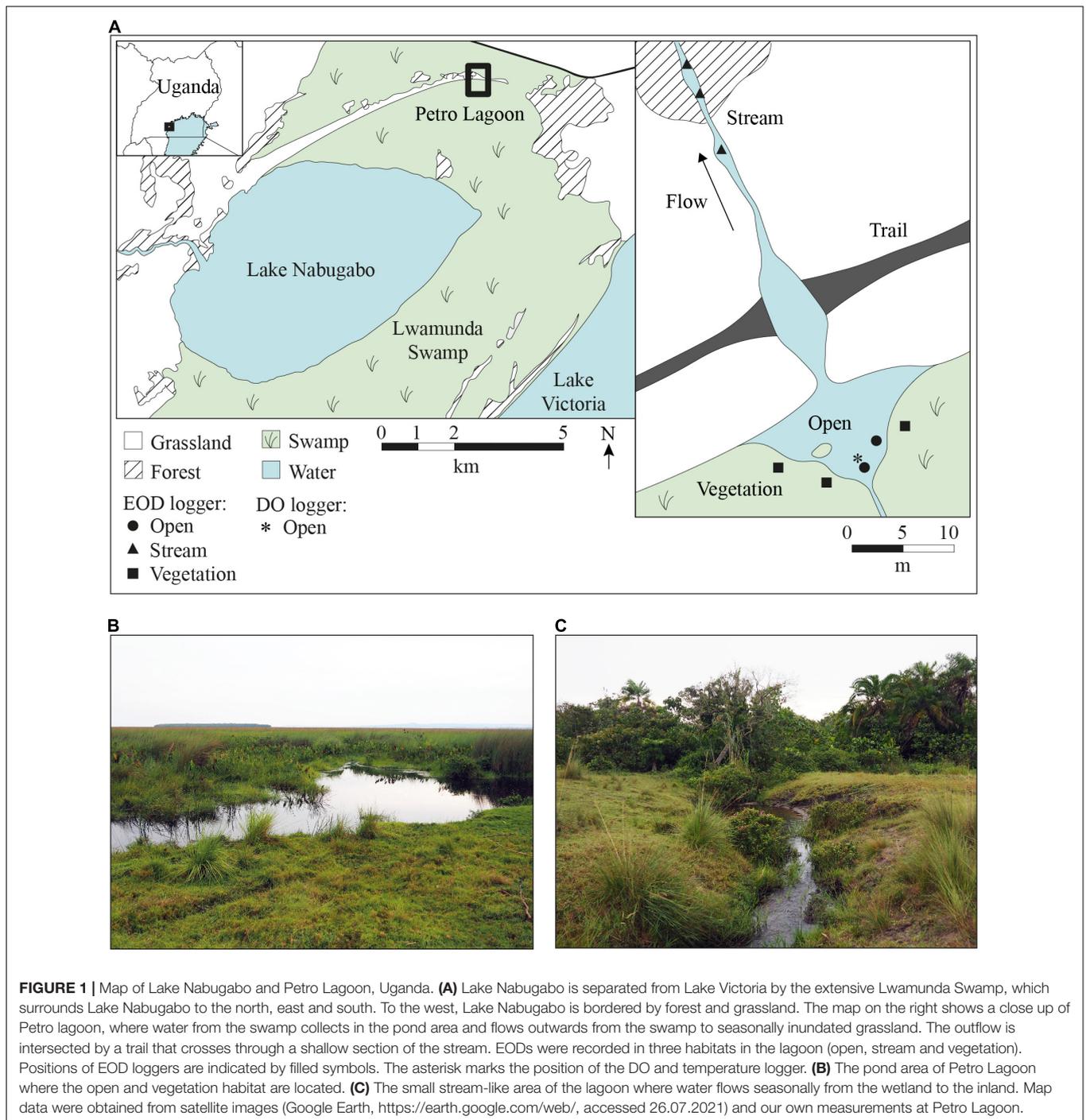
Laboratory Activity Measurements

Activity of laboratory-housed *Marcusenius victoriae* and *Petrocephalus degeni* was measured at Humboldt-Universität zu Berlin, Germany. The fish were wild caught in the Lwamunda Swamp that surrounds Lake Nabugabo in Uganda (**Figure 1**) and transferred to the animal housing facility of the Institut für Biologie of Humboldt-Universität zu Berlin, where they were held under controlled conditions for at least one year prior to experiments. *Marcusenius victoriae* were housed individually in 70 l tanks, and *P. degeni* were kept in groups of up to three fish in 70 l tanks. The light regime was set to a 12:12 h light:dark cycle with 30 min dusk/dawn periods during which light levels gradually transitioned between light and dark. All fish were in non-breeding condition.

Activity was quantified in a shuttle-box system (**Figure 2**; Loligo Systems Inc., Viborg, Denmark). The shuttle-box system consisted of two circular compartments (diameter of 50 cm each), that were connected by a central passage (8.5 cm wide and 14 cm long). Two opaque PVC tubes (5.5 cm inner diameter, 16 cm length) were placed symmetrically, one per compartment, to serve as shelter for the fish during the experiments. A piece of plexiglas was glued to the bottom of

the shelter tubes to secure their position against disturbances. Water temperature was maintained by a thermostat (ITC-308, Shenzhen Inkbird Technology Co., Ltd., Shenzhen, China) that controlled the power supply to two silicone rubber heating mats on either side of the shuttle-box system and one heat radiator that was placed near the setup. The temperature sensor of the thermostat was submerged in the passage between the two compartments of the shuttle-box system. Two pumps (Universal Pumpe 1048, EHEIM GmbH & Co., KG, Deizisau, Germany) created a weak circular current in both compartments to homogenize temperature gradients in the system. The shuttle-box system rested on a self-constructed LED panel, which illuminated the system from below with white light during the day and infrared light during the night. The LED panel was controlled by a programmable LED timer (TC420, Shenzhen Leynew Technology Co., Ltd., Shenzhen, China). The light:dark cycle was set to synchronize with the light regime in the animal housing facility. Light intensity in the shuttle-box was ca. 48 lux during the light phase and 0 lux during the dark phase (**Supplementary Figure 2**). During the dark phase, the setup was illuminated with infrared light (940 nm wavelength) to enable video tracking of the animals. A camera (Grasshopper3 GS3-U3-41S4C-C 1, Teledyne FLIR LLC., Wilsonville, OR, United States) was mounted above the shuttle-box to record swimming activity of the fish. Videos were recorded at sample rates of 25–40 frames per second using Matlab R2018. To minimize disturbance, the setup was visually isolated from the surrounding area with lightproof fabric that was mounted on an aluminum frame around the shuttle-box system, LED panel, and camera. A Faraday cage made of steel mesh was mounted on the same aluminum frame and connected to an electric ground to reduce electric noise. EODs were recorded with carbon rod electrodes that were submerged in both compartments of the shuttle-box. During experiments with *M. victoriae*, one pair of electrodes was used in each compartment. Due to the smaller peak-to-peak amplitude of EODs of *P. degeni*, two pairs of electrodes in each compartment were necessary to reliably record their EODs during activity measurements. EODs were band-pass filtered (100 Hz – 20 kHz), amplified (10 x gain, DPA-2FS, NPI, Germany), digitized at a sample rate of 50 kHz (NI-PCI 6259, National Instruments, Austin, TX, United States), and stored on a computer using Matlab R2018. Videos and EOD recordings were synchronized using a LED light on the side of the LED panel, which signaled the beginning of each new EOD recording.

For each trial, one fish was introduced in a randomly chosen compartment of the shuttle-box in the late afternoon, before the onset of the dark phase, and left undisturbed for 42 h. Over the duration of the trial, movements and EOD activity were recorded continuously. After conclusion of the trial, the fish was removed from the shuttle-box system, weighed and measured, and returned to its home tank. Between two trials, the shuttle-box was cleaned with salt water and rinsed to remove residues from the previous trial. All experiments were approved by the German Landesamt für Gesundheit und Soziales (project number G0278/17).

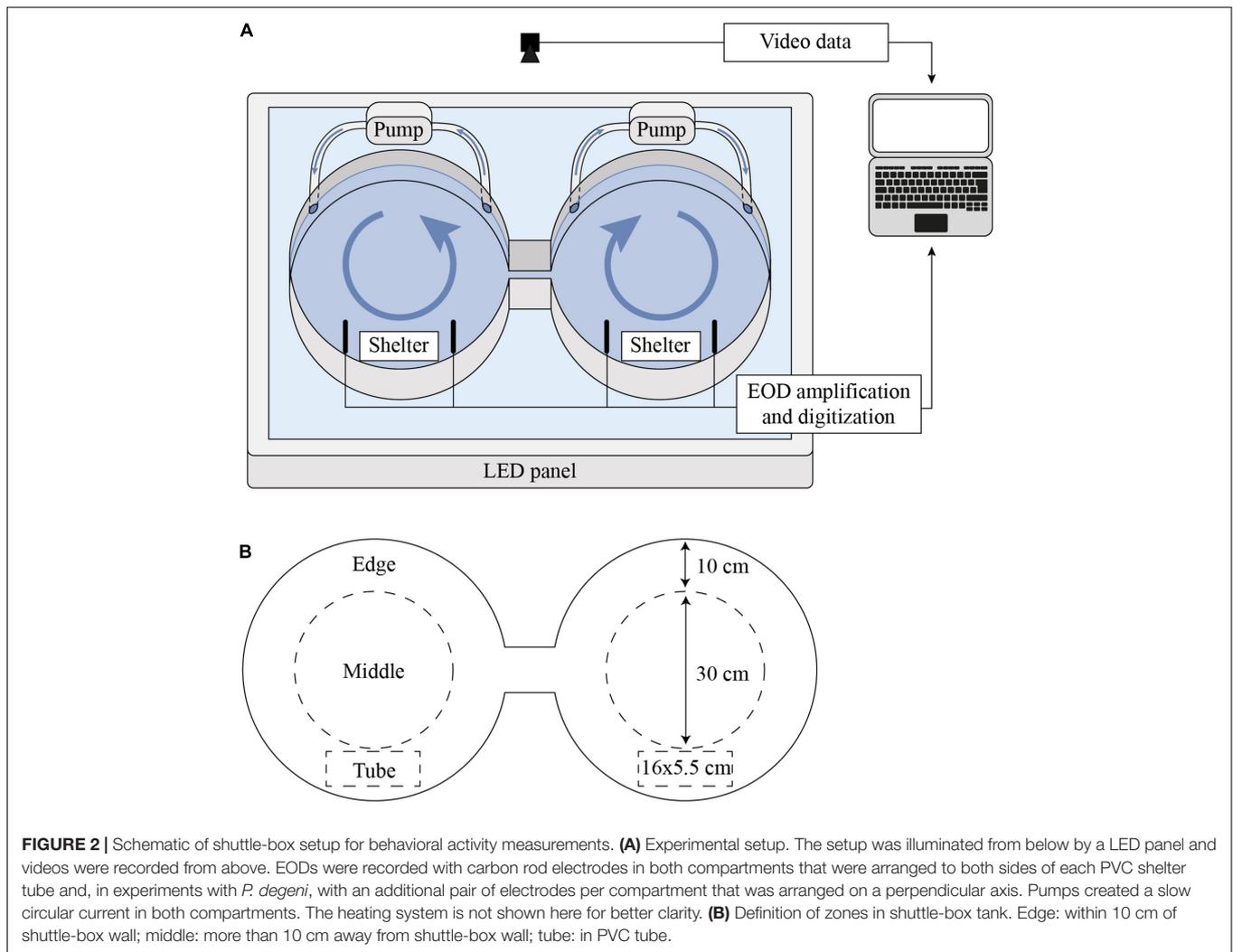


Shuttle-Box Data Analysis

Videos recorded from the shuttle-box were overlaid with a mask to obscure the parts of the image that did not show the shuttle-box system and increase tracking speed using FFMPEG ver. 4.4¹. Fish position was then tracked using the Biotracker 3 software (Mönck et al., 2018). The resulting dataset was further processed using R. High-velocity jumps of the track position (>400 cm/s)

¹<https://ffmpeg.org/> (accessed December 2021).

that occurred, e.g., when fish traversed their opaque shelter tubes or when the tracking position was transiently lost, were corrected by connecting the two positions before and after the jump with a series of equally interspaced steps. Small jitters of the track position were then smoothed using a second-order Savitzky–Golay filter (Savitzky and Golay, 1964). Tracking data were annotated with categorical information about the position of the fish based on the x and y coordinates of the track position. For this, three zones in the shuttle-box tank were



defined: shelter tube (tube), within 10 cm of the edge (edge), more than 10 cm away from the edge (middle, **Figure 2B**). To quantify swimming behavior, the mean swimming speed and the percentage of time spent in the tube, middle, and/or edge of the shuttle-box system were summarized for every 10 min of the trial.

EODs were extracted offline from shuttle-box recordings using Python ver. 3.8.8² with a custom-written Python script and peak-finding functions from the Thunderfish library³. Signals were identified using a peak-finding algorithm, which detected the positive and negative peak of each EOD pulse above a preset amplitude threshold of 0.1 V. A short data fragment (1 ms) centered around the zero crossing of each EOD was extracted, and sample rate was interpolated to 200 kHz for waveform analysis. Several EOD features were extracted from each EOD: peak-to-peak duration, peak-to-peak amplitude, amplitude ratio of positive/negative peak, and the frequency of the highest power of the FFT-transformed pulse. To quantify changes in

electric signaling during the trial, EOD rate, inter-pulse-interval coefficient of variation (IPI CV), EOD amplitude CV, and EOD waveform features were summarized for every second and every 10 min of the trial.

For analysis of location preference, resting EOD rate, and the correlation of EOD rate and velocity, only data from the last 24 h of each trial were used to reduce the effect of acclimation to the shuttle-box system. Location preference was computed as the percentage of total time that fish spent at different locations of the shuttle-box. Resting EOD rate was calculated from sequences of the recording when fish spent at least 5 s in their shelter tube and EOD amplitude remained constant (coefficient of variation < 0.12), suggesting low locomotor activity (Silva et al., 2007).

In situ Recordings Study Site

We recorded EOD activity in the natural habitat of *M. victoriae* and *P. degeni* between July and September 2019 in the Lwamunda Swamp, a wetland surrounding Lake Nabugabo in Uganda

²<https://www.python.org/> (accessed December 2021).

³<https://github.com/bendalab/thunderfish> (accessed December 2021).

(Figure 1). Separated from Lake Victoria about 5000 years ago (Stager et al., 2005), Lake Nabugabo is a small satellite lake (surface area = 33 km², mean depth = 3.13 m, Nyboer and Chapman, 2013) with a unique composition of fish species, such as a small number of haplochromine cichlid species that are endemic to Lake Nabugabo and nearby satellite lakes (Trewavas, 1933; Greenwood, 1965; Kaufman and Ochumba, 1993) and four species of mormyrid weakly electric fishes (Ogutu-Ohwayo, 1993; Chapman et al., 2002). In the years following the introduction of the predatory Nile Perch in the 1960s (Ogutu-Ohwayo, 1993; Pringle, 2005), Lake Nabugabo suffered a dramatic decline or disappearance of several native species from the waters of the main lake (Ogutu-Ohwayo, 1993; Chapman et al., 2003). The lake is surrounded by an extensive wetland area (Lwamunda Swamp), which is dominated by the emergent grass *Miscanthidium violaceum* that transitions to water lilies (*Nymphaea lotus* and *N. carulea*) or hippo grass (*Vossia cuspidata*) at the lake edge (Chapman et al., 1996a; Chrétien and Chapman, 2016). Various fish species occur deep within the wetland (see species list in Chapman et al., 1996b), including *P. degeni* and *M. victoriae* (Chapman et al., 1996b, 2002; Chapman and Hulen, 2001; Moulton et al., 2020). These fishes are protected from predation by Nile perch, as this species does not penetrate the dense swamp and is sensitive to hypoxia (Chapman et al., 2002). Inundation levels, water temperature and DO in the wetland show seasonal and diel variation, though DO remains generally low (previously reported diurnal ranges: 1.06–2.63 mg O₂ L⁻¹, Reardon and Chapman, 2008; 0.69–0.82 mg O₂ L⁻¹, Moulton et al., 2020), and water conductivity is very low (10–20 μS cm⁻¹, measured manually during sampling). All research conducted in Uganda was approved by the Uganda National Council for Science and Technology (research clearance nr. 10601).

Electric Fish Loggers

We developed an autonomous data-logging device to record electric signals in the natural habitat of weakly electric fishes. The electric fish logger consists of a Teensy 3.5 microcontroller board (PJRC.COM, LLC., Sherwood, OR, United States) that is connected to a DS3231 real-time clock module (AZ-Delivery Vertriebs GmbH, Deggendorf, Germany) for timekeeping functionality, and powered by four AA batteries. The electronic components of the logger are housed in a PVC tube with an inner diameter of 45 mm, that is sealed on one side with a glued-on lid and on the other side with a screw lid, which allows replacement of batteries and the microSD card. Two small carbon disks (1 cm diameter, 4 mm long) serve as electrodes to measure EODs. The disks are glued into the lids of the logger housing using aquarium silicone and connected to the analog-digital converters of the Teensy board via copper wire.

The logger continuously records differential voltage through its electrodes with a dynamic input range between –3.3 V and +3.3 V. Voltage data were digitized at a sample rate of 100 kHz with a 12-bit resolution, and stored on a microSD card. The program for the logger was written using the Arduino IDE⁴ and

the Teensyduino plugin⁵. The code for the logger program has been archived and is maintained online on GitHub, alongside a more detailed documentation⁶.

The detection range of the electric fish logger depends on the amplitude of the signal that is generated by the fish. Due to the dipole character of the electric field, the recorded EOD amplitude depends on the distance and the position of the fish relative to the electrodes (see Benda, 2020 for a comprehensive review of electric field geometry). As the two poles of the electric field are located on the head-to-tail axis of the fish, EOD amplitude is largest when the measurement electrodes align with this axis, and practically reaches zero when the fish is perpendicular to the line connecting the two measurement electrodes. Thus, there is no fixed detection range for the loggers, and we rather estimated detection probability. To do this, we recorded freely swimming specimens of each species ($n = 4$ per species, see **Supplementary Material**) in a rectangular tank (200 cm × 100 cm). Detection probability decreased with distance, following an exponential decay function, and was overall lower for *P. degeni*, approaching zero at 50 cm radial distance from the logger (**Supplementary Figure 3**). Detection probability for EODs of *M. victoriae* reached about 10% at the maximum distance of 180 cm. All fish used for detection probability estimation in the lab were in non-breeding condition.

In situ Electric Organ Discharges Sampling

Eight electric fish loggers were deployed in a small lagoon (Petro Lagoon, 0°19'07"S, 31°56'48"E) in the Lwamunda Swamp in three different habitats: under floating vegetation with ca. 1 m distance to the edge of vegetation cover (vegetation, $n = 3$), under the open water surface of the lagoon with at least 1 m distance to the nearest vegetation (open, $n = 2$), and in the middle of the small stream-like area of the lagoon where water flows seasonally from the wetland to the inland (stream, $n = 3$). These habitats were chosen to capture a variety of environmental conditions that is representative of the conditions experienced by fish in the lagoon (**Table 1**). To secure the logger position against perturbations, each logger was attached to a stick that was driven firmly into the ground. Each logger was placed approximately in the middle of the water column and with at least 3 m distance to the nearest logger.

In situ recordings were made on six sampling sessions in 2019 (July: 23–24 and 29–30, August: 8–9 and 21–22, September: 2–3 and 19–20). Electric fish loggers were deployed in the morning and left to record continuously for at least 24 h. After retrieval of the loggers, EODs were extracted from recordings as described above, using Python ver. 3.8.8 (see footnote 2, accessed December 2021) with a custom-written Python script and functions from the Thunderfish library (see footnote 3, accessed December 2021). Only EODs with peak-to-peak amplitudes above 0.066 V (1% of the dynamic range of the logger) were extracted. EODs were then grouped together into encounters based on their zero-crossing timestamp using R ver. 4.1.0⁷. An

⁵<https://www.pjrc.com/> (accessed December 2021).

⁶<https://github.com/muchaste/EOD-Logger> (accessed December 2021).

⁷<https://www.r-project.org/> (accessed December 2021).

⁴<https://www.arduino.cc/> (accessed December 2021).

TABLE 1 | Characteristics of different habitats in Petro Lagoon situated in the Lwamunda Swamp of the Lake Nabugabo System.

Habitat	Loggers (n)	DO	Water flow	Water depth (cm) (cm)	Vegetation cover	Shelter options
Vegetation	3	Low	Very low	33 (22 - 45)	Full cover by swimming mats of vegetation	Structurally complex root masses
Open	2	Low	Very low	66 (56 - 77)	No cover	No shelter
Stream	3	Low	Continuous	33 (12 - 55)	Shaded by overhanging trees and shrubs	Vegetation and roots along the stream edges

DO, dissolved oxygen; Water depth is represented as mean (range).

encounter was defined as a coherent EOD pulse train with at least 10 pulses and a maximum inter-pulse interval (IPI) of 5 s. These selection criteria served to eliminate very brief and/or erroneous fish detections that occurred due to electrical noise, e.g., through lightning discharges. For each encounter, EODs were assigned to either *M. victoriae* or *P. degeni* based on their EOD waveform, using mixture discriminant analysis (MDA) and EOD features. To create MDA models, EOD features from fish that had been recorded under laboratory conditions were used (see **Supplementary Material**). Three features, peak-to-peak duration, peak 1/peak 2 amplitude ratio, and the frequency of the highest power of the FFT-transformed pulse, were sufficient for robust species discrimination with a fidelity of 98.3% (**Supplementary Table 1**). The MDA model was then applied to predict the species for each EOD pulse in the field recordings. After species prediction via MDA, the EOD pulse train of each encounter was inspected visually to determine the number and verify the species of the fish. Encounters with single fish that could not be assigned with confidence (i.e., less than 70% of pulses could be assigned to either species) were removed from analysis.

As individual fish of a given species could not be identified unambiguously based on their EOD features, it is likely that some animals were encountered multiple times. This is even more likely for *M. victoriae*, which have been described as territorial (Carlson, 2016). Although, in theory, absolute animal densities may be estimated despite double counting of individuals (Campos-Candela et al., 2018; Follana-Berná et al., 2020), the data required to satisfy the assumptions underlying such methods (e.g., fish must display home ranging behavior and home range centers must be homogeneously distributed, Campos-Candela et al., 2018) are not available for this study system. Thus, data on fish distribution are presented as frequency of encounters, which depends on fish activity as well as fish density. Frequency of encounters was calculated as the total number of fish that were encountered per logger over intervals of 30 min. Duration of encounters (from first to last EOD) and EOD rate during encounters were extracted to compare encounter characteristics between habitats and periods of the diel cycle. For the comparison of encounter characteristics, only events with a single fish were used, as they occurred most consistently across time and space.

In situ Temperature and Dissolved Oxygen Sampling

One oxygen and temperature logger with optical oxygen sensor (miniDOT, PME, Vista, CA, United States) was placed in the

open habitat of the lagoon to record water conditions on the same sampling days as *in situ* EOD recordings were made. Water temperature and DO concentration were sampled at least every 30 min for the duration of EOD recordings. After each sampling day, data were collected from the logger, and the first and last 30 min of measurements were deleted to remove disturbances in the measurements that were caused by placing and retrieving the logger. Previous manual measurements that were taken during the daytime at this site between 2005 and 2018 showed that temperature varies on average by $0.2 \pm 0.5^\circ\text{C}$ and air saturation varies by $1.8 \pm 7.9\%$ between the water surface and at a water depth of 50 cm ($n = 690$ measurements). As we took the measurements for this study in the middle of the water column, we expect our values to be representative of large parts of the water column where the fish are located. In addition to continuous measurements, diurnal temperature and DO were recorded in all habitats twice per sample day using a handheld meter (Handy Polaris, OxyGuard, Farum, Denmark).

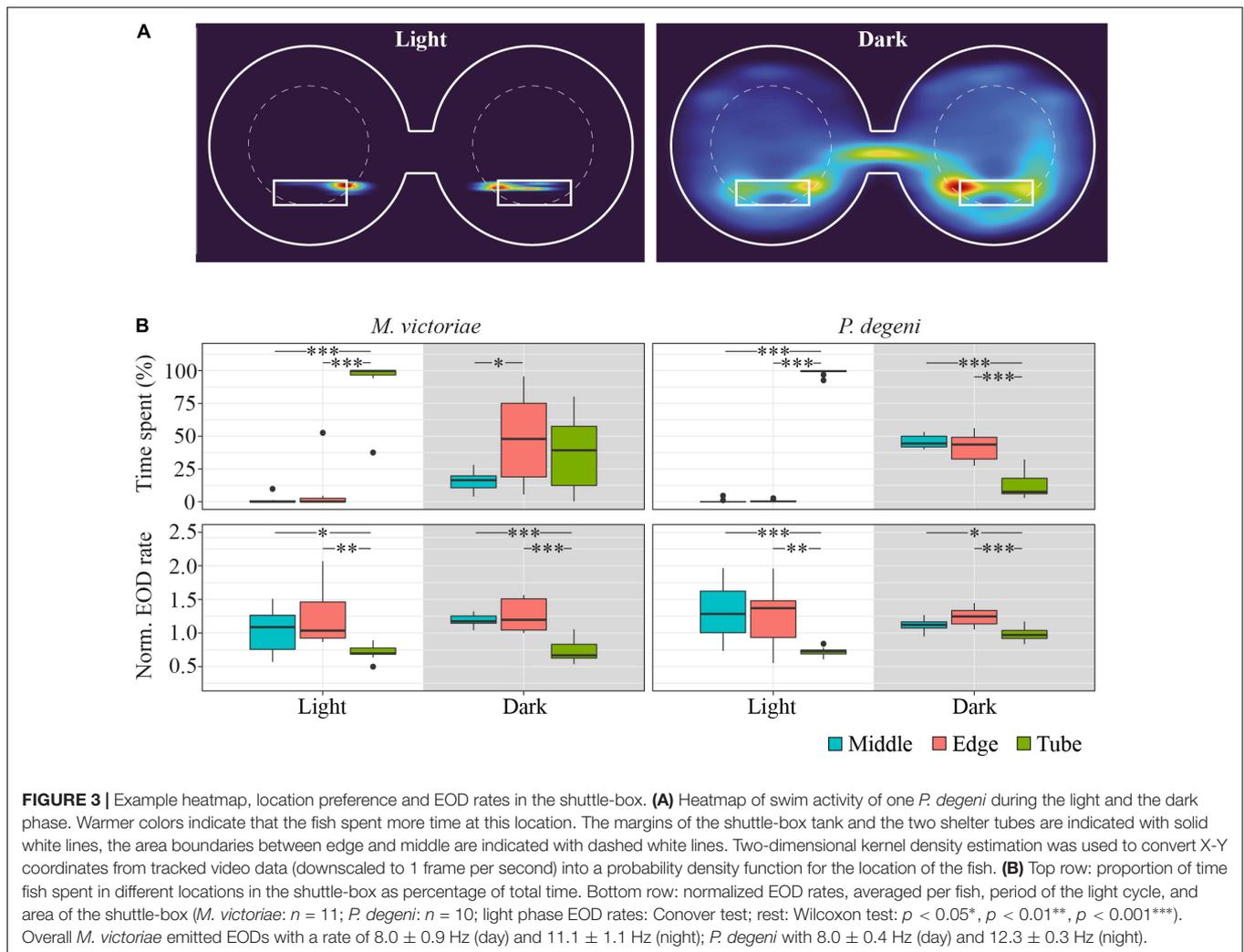
RESULTS

All values are represented as mean \pm standard deviation (SD) if not otherwise stated.

Activity Patterns in the Laboratory

The activity patterns of *M. victoriae* and *P. degeni* in the lab corresponded closely to ambient light levels, with long phases of inactivity and strong shelter preference during the light phase and increased activity and exploration behavior during the dark phase of the trial (**Figure 3**).

During the light phase of the trial, *Marcusenius victoriae* spent $93.1 \pm 18.5\%$ and *P. degeni* spent $98.7 \pm 2.4\%$ of the time in a shelter tube, which decreased during the dark phase to $36.4 \pm 27.5\%$ and $12.5 \pm 10.0\%$ percent, respectively. During the dark phase, *M. victoriae* showed no preference for either shelter tube or unsheltered areas of the shuttle-box (edge and middle). However, when fish were located outside of the shelter tube, they spent significantly more time close to the edge of the shuttle-box than in the middle. Throughout the light cycle, *M. victoriae* emitted EODs at lower rates in the shelter tube than in the unsheltered areas of the shuttle-box. *Petrocephalus degeni* spent significantly more time in the unsheltered areas of the shuttle-box during the dark phase without a preference for the edge or



the middle of the shuttle-box tank. Similar to *M. victoriana*, *P. degeni* emitted EODs at lower rates in the shelter tube during the light phase. However, and in contrast to *M. victoriana*, there was no difference in EOD rates between tank areas during the dark phase (Figure 3B).

Swim speed and EOD rate of both species increased sharply during the 30-min dusk period, peaked at the onset of complete darkness, and remained at elevated levels for the entire duration of the dark phase (Figure 4A). The dark phase proportion of the total distance that fish swam within 24 h was $96.3 \pm 7.8\%$ for *M. victoriana* and $97.7 \pm 4.6\%$ for *P. degeni*. There was no evidence of anticipation of the dark phase (i.e., no increase of EOD rate or swim activity before the dusk period). During the light phase, EOD rate decreased steadily in contrast to swim speed, which dropped quickly close to 0 body lengths per second ($BL s^{-1}$) at the onset of the light phase and remained there until the dusk period. Despite this difference, EOD rate was overall positively correlated with swim speed throughout the light and dark phases for both species (linear regressions: $p < 0.001$; Figure 4B).

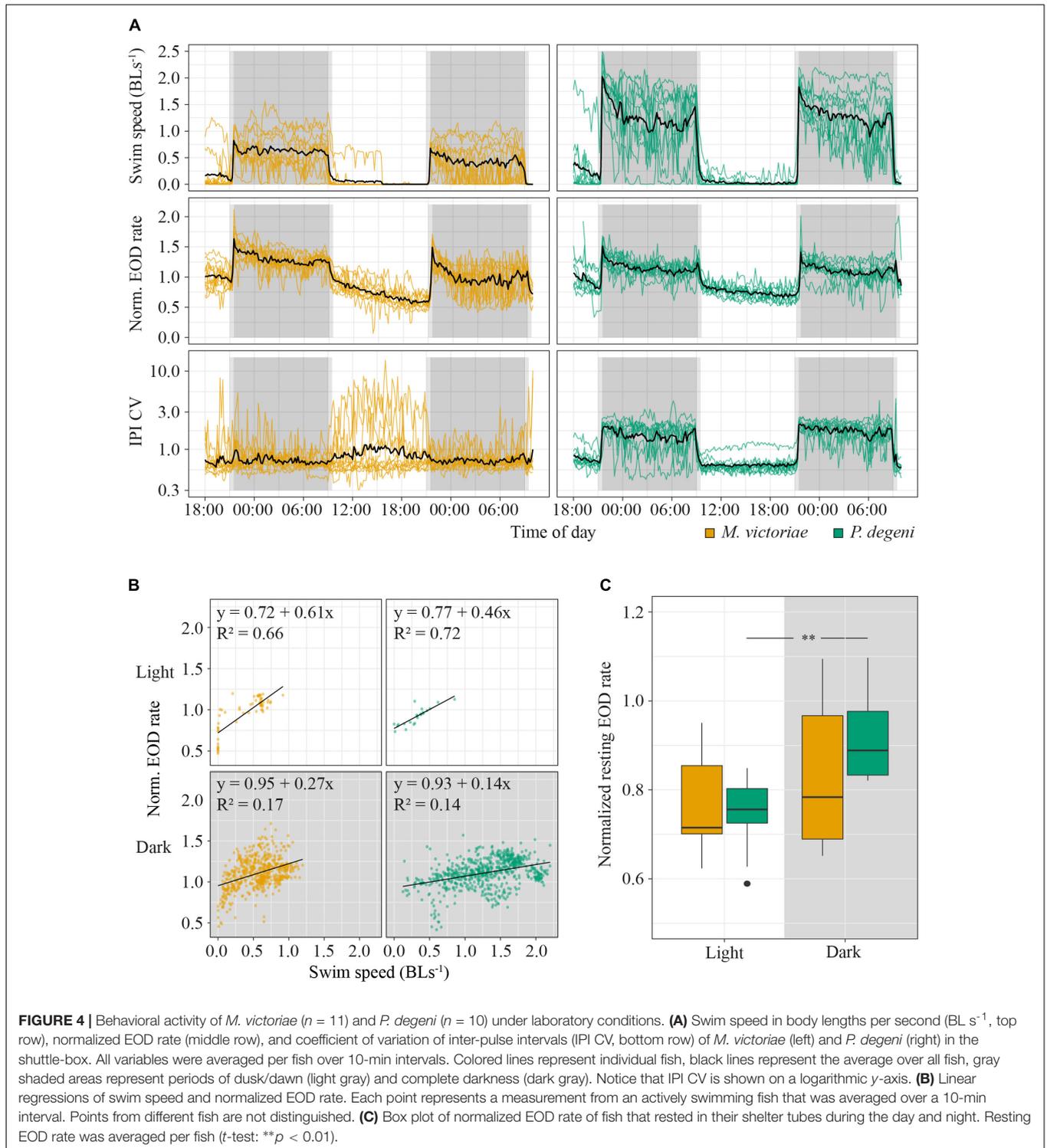
There were some differences between species in swim and EOD activity. Swim activity of *P. degeni* was significantly higher

than that of *M. victoriana* during the dark phase (1.30 ± 0.40 vs. $0.44 \pm 0.28 BLs^{-1}$, Wilcoxon test: $p < 0.001$), and *P. degeni* increased swim speed and EOD rate at the end of the dark phase, an effect that was not as prominent in *M. victoriana*. IPI coefficient of variation (IPI CV) of *P. degeni* showed a clear diel pattern indicating that EOD rate was more variable during their active phase. By contrast, IPI CV of *M. victoriana* did not differ between light and dark phase, and some individuals showed greatly irregular IPIs during the inactive phase, mostly due to longer cessations of EOD generation. The resting EOD rate of *P. degeni* was significantly higher at night than during the day (t -test: $t = -3.57$, $df = 9$, $p < 0.01$; Figure 4C). This effect was not observed in *M. victoriana*.

Environmental and Behavioral Patterns at Petro Lagoon

Temperature and Dissolved Oxygen

Temperature and DO in the open habitat of the Petro Lagoon fluctuated over the diel cycle (Figure 5A). DO reached minimum values at night ($5.1 \pm 5.4\%$ air saturation at 11.5 h after sunset)



and increased in the morning. Rainfall and/or disturbance of the water surface is visible as peaks in DO values and contributed to the increase of mean DO in the morning. Water temperature followed a more pronounced oscillation than DO, reaching its maximum in the late afternoon ($24.9 \pm 1.1^\circ\text{C}$ at 3.5 h before sunset) and its minimum in the early morning ($21.6 \pm 0.7^\circ\text{C}$

at 0.5 h after sunset). Day length remained constant throughout the sampling period (12:06 – 12:07 h, Sunrise: 06:47 – 06:47 am, Sunset: 06:50 – 07:03 pm⁸).

⁸<https://www.worldweatheronline.com/masaka-weather-history/masaka/ug.aspx> (accessed January 2022).

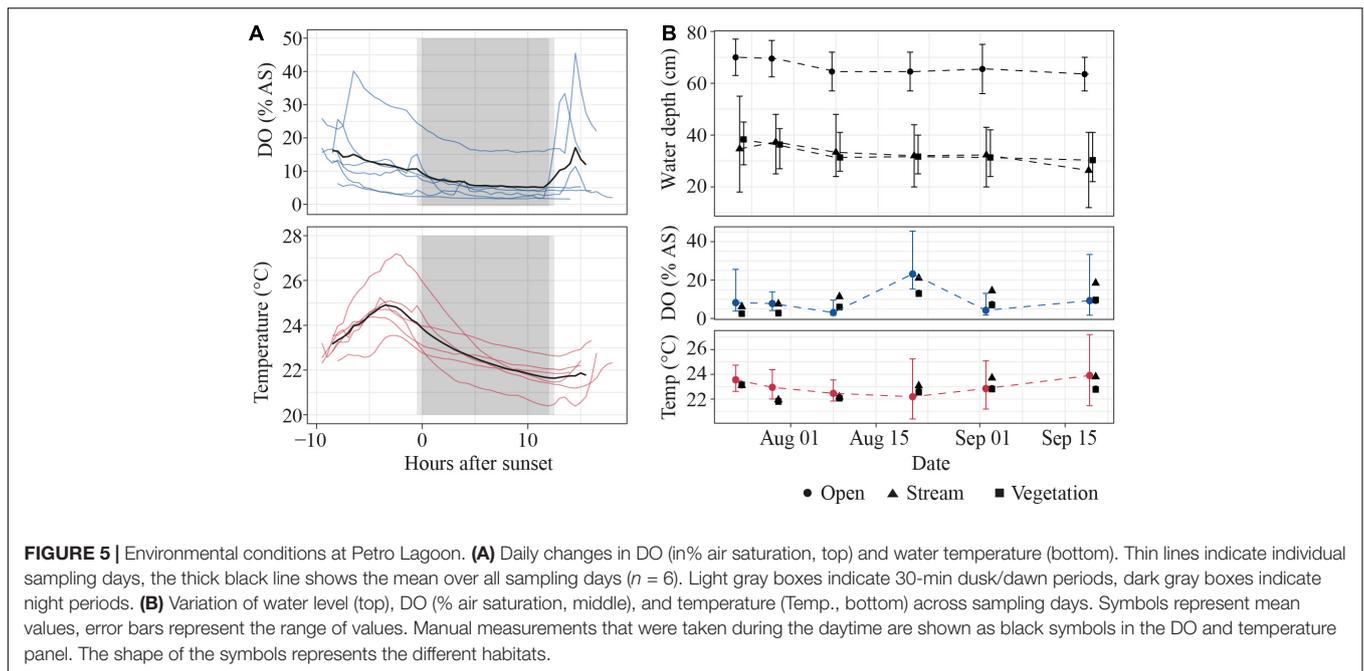


TABLE 2 | Average number of encounters, EOD rates, and durations, grouped by species, habitat and phase of the diel cycle.

Phase	Species	Open	Stream	Vegetation
Encounters per 30 min				
Day	<i>M. victoriae</i>	–	–	0.4 ± 1.1
	<i>P. degeni</i>	–	0.1 ± 0.8	0.9 ± 2.7
Night	<i>M. victoriae</i>	2.2 ± 4.2	–	1.8 ± 3.4
	<i>P. degeni</i>	0.3 ± 1.6	0.4 ± 1.5	1.8 ± 3.9
EOD rate (Hz)				
Day	<i>M. victoriae</i>	–	–	10.3 ± 4.3
	<i>P. degeni</i>	–	16.3 ± 6.3	12.9 ± 6.9
Night	<i>M. victoriae</i>	12.1 ± 6.6	–	10.4 ± 5.4
	<i>P. degeni</i>	16.6 ± 6.1	15.6 ± 4.8	12.1 ± 4.7
Duration (s)				
Day	<i>M. victoriae</i>	–	–	25.6 ± 17.6
	<i>P. degeni</i>	–	8.7 ± 7.6	16.5 ± 15.5
Night	<i>M. victoriae</i>	13.5 ± 12.1	–	25.7 ± 16.9
	<i>P. degeni</i>	10.7 ± 9.4	10.5 ± 8.9	16.7 ± 10.9

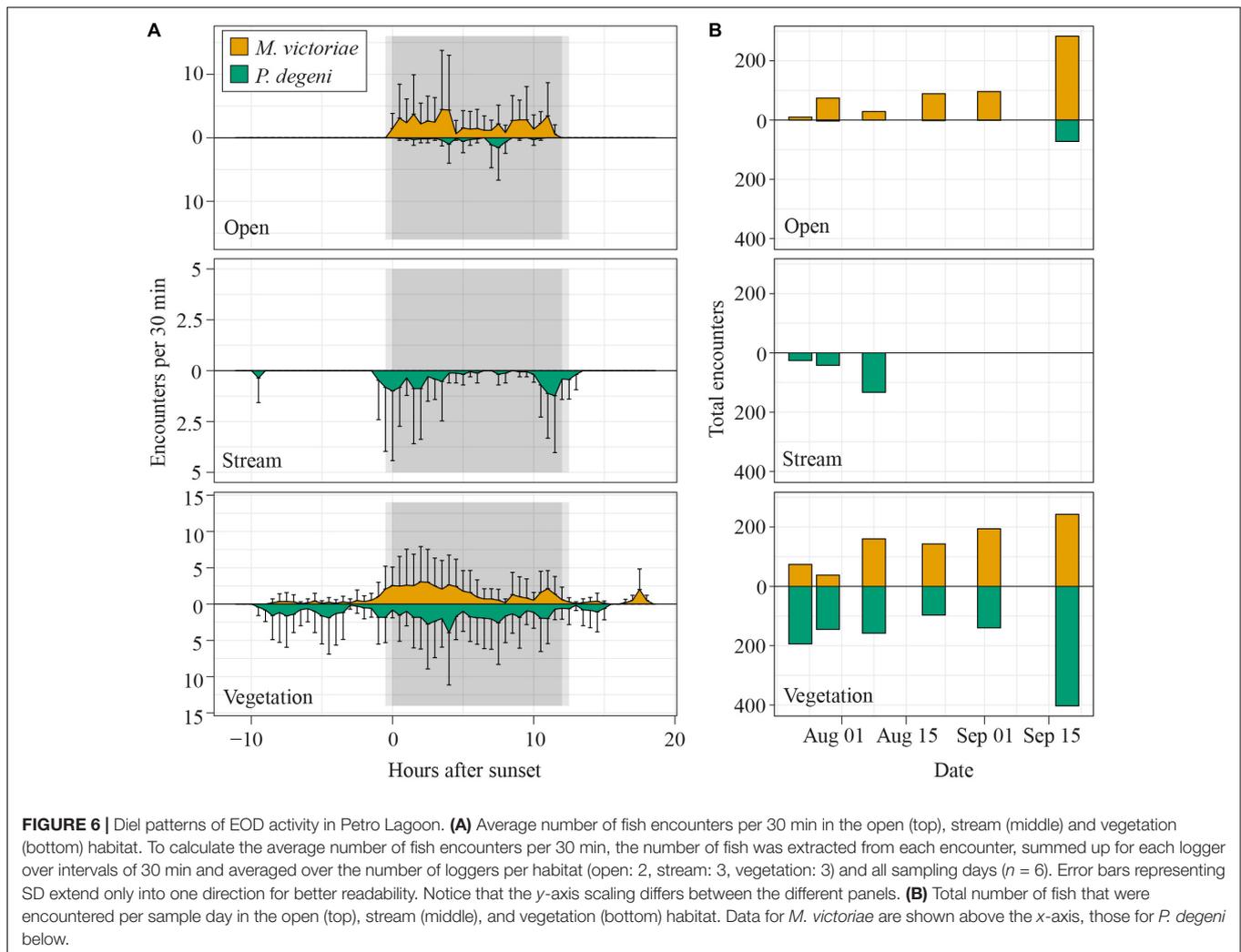
EOD rates and durations were extracted from encounters with single fish. Values are represented as mean ± SD.

Across sampling days, DO was highest on August 21st, due to continuous rainfall on that day, but remained low on average ($9.2 \pm 7.3\%$ air saturation) and was extremely low on August 8th ($2.7 \pm 1.4\%$, **Figure 5B**). Daily water temperature remained at a relatively constant average value ($23.0 \pm 0.6^\circ\text{C}$) despite diel fluctuations. Water depth also remained relatively constant in all habitats and was highest in the open habitat. Manual measurements that were taken during the day showed little difference in temperature and DO between the open and vegetation habitat. However, DO and temperature tended to be slightly but systematically higher in the stream habitat (by $6.4 \pm 2.4\%$ air saturation and $0.4 \pm 0.7^\circ\text{C}$, **Figure 5B**) than other areas of the lagoon.

Presence of Electric Fish in the Different Habitats

We collected more than 1,122 h of electric recordings in the open, stream and vegetation habitat at Petro Lagoon between July 23rd and September 20th 2019. We registered 2849 encounters with at least one *M. victoriae* and/or *P. degeni*, most of which happened during the night (2218). Both species were encountered equally often (*M. victoriae*: 1433, *P. degeni*: 1416). By far the highest number of encounters was recorded in the vegetation habitat (1137 and 852, respectively), followed by the open habitat (581 and 78, respectively), and the stream (0 and 201, respectively).

The frequency with which encounters occurred in the different habitats varied between species and periods of the



diel cycle (Table 2 and Figure 6A). In the open habitat, both *M. victoriae* and *P. degeni* were encountered only at night, and *M. victoriae* accounted for the majority of the nocturnal encounters. Under the floating vegetation, both species were encountered throughout the diel cycle. However, the frequency of encounters with *M. victoriae* increased more than fivefold from daytime to nighttime, whereas *P. degeni* were encountered more continuously during the day and the night under the floating vegetation (Table 2). In the stream habitat, only *P. degeni* were encountered, and primarily at night.

The number of daily fish encounters varied considerably across sampling days (Figure 6B). Encounters with *M. victoriae* increased in the open habitat and vegetation habitat from 84 to 526 encounters. Numbers of encounters with *P. degeni* remained relatively constant under the floating vegetation except for a peak of 403 encounters on the last sampling day. In the stream habitat, *P. degeni* was encountered only during the first three sampling days, and in the open habitat only on the last sampling day. Overall, 35% of all fish encounters were made on the last sampling day.

Co-occurrence of Fish

In 18.7% of encounters, more than one fish was detected (co-occurrence; Figure 7A). On average, the proportion of encounters during which multiple *M. victoriae* were detected simultaneously was higher at night ($17.4 \pm 10.9\%$ of encounters) than during the day ($2.0 \pm 2.8\%$; *U*-test: *U* = 2, *p* < 0.05). *Petrocephalus degeni*, likewise, co-occurred more often at night ($10.8 \pm 8.4\%$) than during the day ($2.4 \pm 4.1\%$; *U*-test: *U* = 3, *p* < 0.05). There was no difference between the two species in the percentage of encounters that included more than one conspecific. In 50.9% of co-occurrences, fish from both species were present.

Encounter Duration and Electric Organ Discharges Rate

Encounter duration and EOD rate differed among habitats and periods of the diel cycle, suggesting that fish displayed higher activity in the open and stream habitat and around sunset and sunrise (Table 2 and Figures 7B,C).

In the vegetation habitat, where most encounters were detected throughout the diel cycle, EOD rates of *M. victoriae*

peaked within one hour of sunset and again shortly before sunrise. EOD rates of *P. degeni* were highest during the day but showed a small peak before sunrise (Figure 7B). These changes were transient and did not lead to elevated nocturnal EOD rates, as were observed in the laboratory. Both species emitted EODs at a lower rate under the vegetation than in the other habitats, both during the day and at night, and encounters lasted longer under the vegetation than in the other habitats (Figure 7C). Overall, the EOD rates of *M. victoriae* in the field were comparable to those from the laboratory (day: 10.3 ± 4.3 Hz vs. 8.0 ± 2.3 Hz; night: 11.1 ± 6.0 Hz vs. 11.1 ± 3.3 Hz). EOD rates of *P. degeni* were significantly higher in the field than in the laboratory during the day (13.0 ± 6.8 Hz vs. 7.7 ± 2.8 Hz, *U*-test: $U = 3069$, $p < 0.01$), but not during the night (13.6 ± 6.8 Hz vs. 11.3 ± 4.8 Hz).

DISCUSSION

In this study, we tracked the activity of two species of mormyrid weakly electric fishes in the laboratory and recorded their diel activity patterns in a chronically hypoxic habitat using newly developed recording devices. In both settings, *M. victoriae* and *P. degeni* showed distinct, daylight-dependent behavioral patterns that were characterized by increased activity and exploration behavior under dark conditions. Diel patterns of co-occurrence suggest that the study species interact socially primarily during the night in their habitat. Although the behavior observed in the laboratory and in the wild was largely congruent, *P. degeni* showed higher daytime activity in naturally dark habitats than in the laboratory, and the increase of activity during the dark phase was much more pronounced and consistent in the laboratory than in the wild for both species. These findings suggest that the activity of the study species depends more on the environmental light conditions than on the phase of the diel cycle. It is likely that sinking nocturnal DO and temperature further affect activity patterns that are more varied in the wild than what is observed in the laboratory.

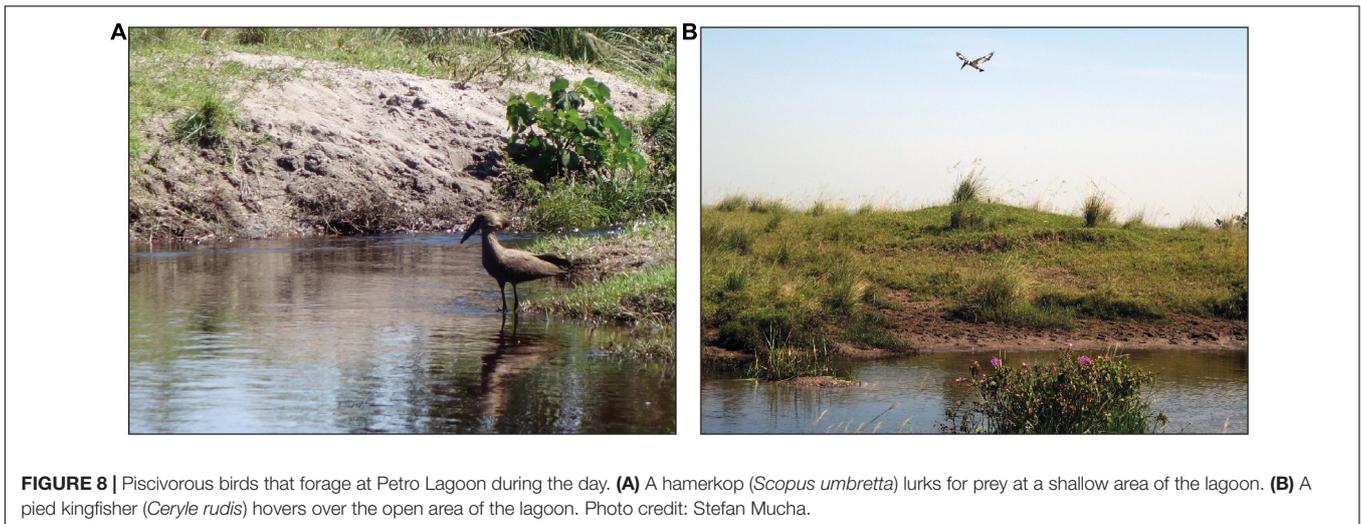
Spatial and Temporal Patterns of Behavior

Habitat Use and Swim Behavior

In the laboratory, fish spent nearly 100% of the time in their shelters during the light phase and increased their behavioral activity with the onset of the dark phase, which resulted in higher swim speed and a change in their movement range from sheltering to active exploration of their environment. In the wild, fish were almost exclusively detected under floating vegetation during the day and dispersed into the open areas of the lagoon at night. Interestingly, *P. degeni* showed a stronger preference for open areas in the shuttle-box during the dark phase than *M. victoriae*, whereas in the wild, *M. victoriae* were encountered more often in the open area at night, and *P. degeni* seemed to prefer the vegetation habitat both during day and night. As the sheltered areas in the shuttle-box were limited to two tubes, it is possible that this was an effect of the overall higher swim activity of *P. degeni* compared to *M. victoriae*. The different activity levels of the two species could also help to explain the fish dispersion

patterns at Petro Lagoon. Given that DO was overall low but highest in the stream habitat, it could have been expected that fish move into the stream at night to reduce hypoxic stress. Thus, it came as a surprise to find that only *P. degeni* were encountered here, and only on the first three sampling days. It is possible that their higher activity level makes *P. degeni* more vulnerable to hypoxia and/or better adapted to an environment with flowing water. The more sluggish *M. victoriae*, on the other hand, might be better adapted to stagnant environments. Another possible explanation for the lack of fish in the stream is that fish had to cross a shallow section of the lagoon in order to reach it. Due to its low water depth, this section may have represented a movement barrier for the larger *M. victoriae* in the beginning of the sampling period. Over the sampling duration, water depth decreased slightly throughout the lagoon, which could have kept *P. degeni* from venturing into the stream on the later sampling days.

The temporal patterns of fish encounters suggest that fish actively moved into the open and stream areas of the lagoon at night and returned to the floating vegetation around sunrise. The transient increase of EOD rates under the vegetation during sunset and sunrise could be a result of this movement activity. This seems to align well with the activity peaks that were observed in the laboratory at the onset and toward the end of the dark phase. The question is, for what purpose do fish emerge at night and venture into unprotected areas? We suggest that fish use the open habitats to forage, interact, and carry out ASR at night at a lower risk of predation (e.g., Hobson, 1973; Nagelkerken et al., 2000; Hammerschlag et al., 2010; Sikkel et al., 2017). Although the low DO in the swamp protects fish from large predators, such as the Nile perch (*Lates niloticus*, Chapman and Chapman, 1998; Chapman et al., 2002), there is some risk of predation during the daytime due to the presence of visually oriented piscivorous birds, such as the hamerkop (*Scopus umbretta*) and the pied kingfisher (*Ceryle rudis*, Figure 8). These predators hunt predominantly in the open and shallow regions of the lagoon (pers. observation), turning them into dangerous territories for fish during the day. Further, the complete absence of mormyrids in the open and stream habitat during the day indicates that there is little diurnal foraging activity in these areas. At night, fish can exploit the untapped resources at a lower risk of predation. The non-visual sensory modality of *M. victoriae* and *P. degeni* facilitates prey capture in the dark (Emde and Bleckmann, 1998; Emde, 1999), and gives them an edge over other visually oriented nocturnal foraging species. Encounter duration and EOD rates suggest that the activity level of fish was higher in the open and stream area than in the vegetation, which aligns well with foraging behavior as increased EOD rates increase the temporal acuity of electrosensory information, and can aid in the localization of prey and/or avoidance of predators. Similar nocturnal exploration and foraging activity has been described before in weakly electric fishes (Lissmann and Schwassmann, 1965; Kruger, 1973; Moller et al., 1979; Friedman and Hopkins, 1996; Henninger et al., 2018; Madhav et al., 2018; Henninger et al., 2020). For example, Henninger et al. (2020) observed in a creek in Panama that three gymnotiform species, *Apteronotus rostratus*, *Eigenmannia humboldtii* and *Sternopygus dariensis*, move actively



only during the night, traveling upstream after sunset and downstream in the second half of the night. In an early study in Brazil, Lissmann and Schwassmann (1965) demonstrated that sandfish (*Gymnorhamphichthys hypostomus*) rest, buried in the sand, during the day and emerge at night to forage and interact. In South Africa, Kruger (1973) found that *Marcusenius macrolepidotus* (formerly *Gnathonemus macrolepidotus*), a close relative to *M. victoriae*, moves at night from bottom waters into the littoral zone, presumably to feed on chironomids. Moller et al. (1979) recorded mormyrids in the Swashi River in Nigeria, which hid during the day in a river inlet and moved actively in and out of the river at night. The behavior of *M. victoriae* and *P. degeni* described here matches these observations well.

We saw an increase in total fish encounters toward the end of the sampling period, especially on the last sampling day. Our last measurements were made just at the onset of the short rainy season, and there was a slight upwards trend in DO and temperature on the three last measurement days. The increase of encounters might be a result of higher behavioral activity due to higher energy availability and temperature. Another intriguing possibility is that the increase of fish encounters was caused by seasonal breeding migrations. Some mormyrid species breed at the onset of the rainy season (Hopkins and Bass, 1981; Kirschbaum, 1995). Decreasing water conductivity, increasing water levels, and artificial rainfall on the surface all promote gonad growth in those species (e.g., Kirschbaum and Schugardt, 2002). Although not much is known about the natural breeding behavior of our study species, it is possible that the increase of encounters with *M. victoriae* and the high number of encounters with *P. degeni* on the last sampling day indicate breeding behavior. This would be an exciting finding, as it would mean that these fish reproduce under severely hypoxic conditions. A longer-term survey of the fish distribution in the Lake Nabugabo system during the rainy seasons, e.g., with electric fish loggers, should give better insights into this important aspect of the ecology of *P. degeni* and *M. victoriae*.

Electric Activity

In the laboratory, EOD rate was closely correlated to swim activity in both species and showed clear diel rhythms. The two species differed in their temporal patterns of EOD generation. *Petrocephalus degeni* emitted EODs at more regular intervals during their inactive phase and became more irregular during their active phase. This was not the case in *M. victoriae*. In contrast, some *M. victoriae* showed greatly irregular IPIs with pauses that exceeded 10 s and could reach up to > 120 s during their inactive phase. Similar differences in EOD generation have been described by Carlson (2016) who found that *M. victoriae* respond to EOD playback with pauses of electric signaling whereas *P. degeni* tend to generate EOD bursts. These differences in pulsing behavior likely reflect a variety of differences in electrosensory anatomy and social behavior between these two species (Carlson, 2016). For example, cessations of EOD generation have been associated with aggressive and submissive behavior (Carlson, 2002), traits that might be more typical of *M. victoriae* (Carlson, 2016). Pausing EOD generation during their inactive phase could reduce their detectability by electrosensory predators and/or aggressive conspecifics.

In the field, EOD rates of *M. victoriae* increased after sunset, however, this effect was much more transient than in the laboratory. The EOD rates of *P. degeni* were highest during the day and showed only a transient increase toward the end of the night. Overall, the clear pattern that was observed in the laboratory could not be reproduced in the field. We identified a variety of factors that may have influenced EOD activity patterns. First, the lower water temperatures likely reduced EOD rates during the night (e.g., Toerring and Serrier, 1978). Second, nocturnal hypoxia could have led to reduced EOD rates (Clarke et al., 2020; Moulton et al., 2020), if it was not compensated for, e.g., by aquatic surface respiration (ASR), during which fish ventilate the well-oxygenated surface water layer (Lewis, 1970; Chapman and Chapman, 1998). Third, *P. degeni* maintained a higher level of activity during the day under the floating vegetation than in the tubes of the shuttle-box. This effect could

not be discerned in *M. victoriae*. It appears that the availability of an extensive sheltered habitat stimulated diurnal activity (e.g., exploration and foraging) of *P. degeni*. A possible factor for the species difference in diurnal activity could be their different social behavior, with the group-living *P. degeni* exhibiting higher diurnal activity than the solitary *M. victoriae*, although this remains speculative.

Social Interaction

Unlike many other fishes, which rely primarily on visual cues for social interaction (e.g., reviewed by Rowland, 1999), weakly electric fishes can use their active electrosense to communicate and interact with conspecifics, and thus are well equipped to do so at night (Moller et al., 1989; Scheffel and Kramer, 1997; Carlson and Hopkins, 2004). The sampling design we used did not allow detailed observation of social interactions, and an in-depth analysis of EOD recordings from co-occurrences was beyond the scope of this study, which focused on the temporal and spatial dynamics of fish behavior. However, some conclusions can be drawn from the statistics of recorded co-occurrences of fish. Here, it is important to consider the different detectability of the two species. While co-occurring *P. degeni* had to be within approximately 1 m of each other to be detected simultaneously in a logger recording, *M. victoriae* could be more than 3 m apart from each other and still be detected together. Thus, based on co-occurrences, the degree of social interaction is likely somewhat overestimated in *M. victoriae* (co-occurrence without interaction) and underestimated in *P. degeni* (detection of one fish out of a group). Notwithstanding these limitations, the fact that co-occurrences increased by 850% (*M. victoriae*) and 450% (*P. degeni*) strongly suggests that fish encountered and interacted with conspecifics more frequently at night. Nocturnal bouts of social interaction have also been described in the phylogenetically distant gymnotiforms and could be a common characteristic of weakly electric fishes (Silva et al., 2007; Stoddard et al., 2007). *Marcusenius victoriae* has been described as a territorial species, which is solitary and displays high intraspecific competition for shelters (Carlson, 2016). Our recordings suggest that territoriality and competition for shelters is most prominent during the daytime, when *M. victoriae* were recorded exclusively in the vegetation, and were alone in ca. 98% of those encounters. During the night, *M. victoriae* seem to show a higher degree of social affiliation and/or acceptance of conspecifics in their proximity. Interestingly, most co-occurrences of *M. victoriae* were recorded in the open habitat, which may suggest that they favor interacting in a more “neutral zone” than in the habitat where fish occupy their shelters during the day. *Petrocephalus degeni*, on the other hand, has been described as a gregarious species (Carlson, 2016), and can be kept in group tanks more easily than *M. victoriae* (pers. observation). There was no difference between the two species in the proportion of conspecific co-occurrences, however, given the considerable difference in detectability, this finding supports the notion that *P. degeni* occurs naturally in social groups.

During most encounters with multiple fish, both species were present. In some cases, the low-amplitude EODs of a *P. degeni* were only revealed due to the presence of another fish whose EOD

amplitude crossed the detection threshold, which was frequently *M. victoriae*. Nevertheless, this implies that both species occur in spatial proximity and likely are connected through interactions and/or competition for resources. More detailed behavioral observations, e.g., using a grid of electrodes (Henninger et al., 2018, 2020; Madhav et al., 2018), could give interesting insights into the nocturnal social behavior of these sympatric species.

Environmental and Endogenous Rhythms

Influence of Light

Behavioral rhythms can be governed by environmental cues and endogenous biological clocks, and the question, which one of these two components drives an observed behavioral rhythm cannot be answered without thorough study of the endogenous circadian rhythms of an organism (Aschoff, 1960). In the laboratory, where temperature and DO were kept constant, behavioral activity of *M. victoriae* and *P. degeni* corresponded closely to ambient light levels: locomotor activity and EOD rate peaked precisely at the onset of darkness. Although activity level was not directly quantified in the field, the patterns of fish encounters corroborate this finding. In the open area where day-night changes in illumination are most pronounced, the number of fish encounters followed a clear diel pattern. In the vegetation habitat where light conditions remain mostly dark throughout the diel cycle, this pattern was less obvious, and *P. degeni* showed the same level of activity during the day and the night. Both observations suggest that light intensity is an important factor for behavioral activity, however, they are insufficient to disentangle the effects of endogenous clocks that are entrained by light and the direct effect of light as environmental cue on the behavior of *M. victoriae* and *P. degeni*.

There was no evidence that fish anticipated the dark phase, which could have served to suggest the existence of a circadian clock (Reebs, 1994). Two findings, however, could indicate the effect of an endogenous rhythm on behavioral activity in *P. degeni*. First, they showed an increase in swim speed and EOD rate toward the end of the dark phase, both in the laboratory and in the field. A similar phenomenon has been documented in *G. petersii* (Bässler et al., 1979). Second, their EOD rate at rest was significantly higher during the night than during the day. A similar increase in nocturnal EOD baseline rate has been found in the pulse-type gymnotiform *Gymnotus omarorum*, which lives under naturally constant darkness (Migliaro et al., 2018). This phenomenon has been hypothesized to be under endogenous control, although this has yet to be confirmed under laboratory conditions. The presence of a circadian rhythm could be tested by subjecting fish to constant light and/or dark conditions for several days while assessing whether free-running behavioral rhythms can be detected (Aschoff, 1960). In a study with the pulse-type gymnotiform *Brachyhyppopomus pinnicaudatus*, Stoddard et al. (2007) found circadian rhythms in electric signal parameters that are likely caused by melanocortin peptides, which act directly on electrocytes, and through serotonergic projections to neuronal pacemaker structures. However, in a recent field study,

Henninger et al. (2020) also found no evidence for anticipation of the active phase in wild gymnotiforms.

Temperature and Dissolved Oxygen

Interestingly, the nocturnal increase of activity and movement range co-occurred with extreme nocturnal hypoxia at Petro Lagoon. In line with previous observations and surveys, which have consistently found both species in this site since the 1990s under hypoxic conditions (Chapman et al., 1996b, 2002; Chapman and Chapman, 1998; Carlson, 2016; Clarke et al., 2020; Moulton et al., 2020), the continuous *in situ* measurements of EODs, DO and temperature show for the first time that these fish remain present, and likely are most active, throughout the most extreme nocturnal hypoxia periods. This is an intriguing finding as, although both species investigated here have been found to be hypoxia-tolerant (Chapman and Chapman, 1998; Clarke et al., 2020; Moulton et al., 2020), the degree of nocturnal hypoxia found here far exceeded their respective physiological thresholds of oxyregulation (P_{crit}). P_{crit} is defined as the oxygen partial pressure at which an organism can no longer maintain a stable rate of oxygen consumption (oxyregulation) and begins to conform to environmental DO (oxyconformation; Beamish, 1964; Ultsch et al., 1978). In the study site, air saturation dropped as low as $2.7 \pm 1.4\%$ (on August 8, 2019), which is well below any P_{crit} measured in swamp-dwelling *P. degeni* (Chapman and Chapman, 1998: ca. 5.8%, Clarke et al., 2020: ca. 7.0%) and *M. victorinae* (Moulton et al., 2020: ca. 9.5%). In fact, mean PO_2 at this site remained below the lowest published P_{crit} for more than 50% of the diel cycle on three of the six sampling days. Ackerly et al. (2018) showed that a DO concentration of ca. 17.5% already negatively affected the critical swim speed and EOD rate of *M. victorinae*. Temperature decreased during the night at Petro Lagoon, which could reduce the rate of metabolic processes and somewhat buffer hypoxic stress. However, it seems unlikely that this effect would suffice to compensate for extremely low nocturnal DO, which suggests that environmental hypoxia significantly limited the performance of both species, particularly during their most active phase. This raises the question as to how these fish manage to maintain and even ramp up their levels of electrical and locomotor activity during extreme hypoxia. One possible explanation is that fish compensate for the nighttime hypoxia by using ASR (Chapman and Chapman, 1998). Since ASR requires that fish have free access to the water surface, fish have to emerge from the swimming vegetation to perform ASR. This might drive the nocturnal migration of both species into the open habitats. At night, ASR could be particularly well suited to increase oxygen supply as the absence of diurnal predators reduces the otherwise high risk of predation (Kramer et al., 1983). A similar behavior has been identified in Amazonian fishes that emerge from their macrophyte cover to perform ASR during periods of severe nocturnal hypoxia (Saint-Paul and Soares, 1987).

The diel fluctuation of DO and temperature could entrain endogenous circadian rhythms, and therefore affect behavioral activity on another level. The circadian clock has been shown to be closely related to the hypoxia-signaling pathway in mammals (e.g., Adamovich et al., 2017) and zebrafish (*Danio rerio*, Egg

et al., 2013; Pelster and Egg, 2018; Sandbichler et al., 2018). Hypoxia-inducible factor 1 α (HIF-1 α) is a key regulator of the physiological hypoxia response. It dimerizes with HIF-1 β under hypoxic conditions and regulates the transcription of genes by binding to hypoxia-responsive elements (Wenger et al., 2005; Schödel et al., 2011). The expression of HIF-1 α is tightly controlled by the circadian clock and follows a circadian rhythm (Egg et al., 2013). On the other hand, hypoxic conditions lead to decreased expression levels of clock genes such as *period1* (Egg et al., 2013; Sandbichler et al., 2018). Adamovich et al. (2017) suggest that, mediated through HIF-1 α , hypoxia is a resetting cue for circadian clocks. In fish that have adapted to chronic environmental hypoxia, such as *M. victorinae* and *P. degeni*, an interesting question for further studies would be, whether adaptation to hypoxia has affected this interaction, or whether the expression of clock genes remains constantly dampened by hypoxia.

Many fish species seem to possess peripheral clocks in their tissues that are light sensitive without the need for specialized light sensing organs such as eyes or the pineal gland (Whitmore et al., 2000; Frøland Steindal and Whitmore, 2019). The finding of such peripheral clocks illustrates that the concept of a centralized “master-clock” that governs rhythmic behavior does not extend to fish, which rather possess a full-body light sensitivity (Frøland Steindal and Whitmore, 2019). As oxygen levels are not homogeneously distributed throughout body tissues, it is likely that these peripheral clocks are differentially affected by hypoxia. Although this has not been shown in electric fish yet, their well-understood neural circuits and non-invasively detectable EODs make electric fishes promising subjects for future studies of biological rhythms and the influence of light, DO and temperature.

Recording Natural Activity Patterns With Electric Fish Loggers

Mormyrids are often considered nocturnal animals, however, this view is at least partially based on laboratory studies (Harder et al., 1964; Moller, 1970; Bässler et al., 1979; Cobert, 1984). As we show here, natural activity patterns can deviate from laboratory activity patterns. A closer look into the literature demonstrates that mormyrids exhibit a variety of natural activity patterns that would not all classify as nocturnal. Using capture by gill net in Loskop Dam, South Africa, Kruger (1973) found that *M. macrolepidotus* migrate at night from bottom waters to the littoral zone. However, based on stomach content analysis, he also concluded that they feed predominantly during the day at the bottom of the reservoir. In the Ivindo River district in Gabon, Hopkins (1980) recorded EODs of 23 mormyrid species in the field and noted that mormyrids in shallow water remained sheltered during the day and made occasional foraging excursions at night whereas fish that lived in deeper waters appeared to move around during the day, as well. Our study shows that *P. degeni* remain active during the day under floating vegetation. In all of these studies, mormyrid activity seems most clearly determined by ambient light levels, and might not follow a diel pattern in continuously dark habitats. This differentiation may seem trivial,

however, it has far-reaching biological implications. Nocturnality suggests a fixed and recurring behavioral rhythm that is likely to be under the control of endogenous oscillations whereas direct light-sensitivity facilitates more opportunistic behavioral patterns and might be independent of endogenous clocks. Understanding the mechanisms that underlie natural activity patterns of fishes is a crucial step to understanding the dynamics of aquatic ecosystems. Weakly electric fishes offer great opportunities in this regard. Their EODs give insight into the activity, habitat use and social interaction of elusive, tropical fishes, that are impossible to gain through visual observation methods. Previous studies have used electrode arrays (Henninger et al., 2018, 2020; Madhav et al., 2018), or single/handheld electrodes (Lissmann and Schwassmann, 1965; Moller et al., 1979; Hopkins, 1980; Friedman and Hopkins, 1996; Migliaro et al., 2018) to record EOD activity of weakly electric fishes in the wild. The methods that these studies employed necessitated the supervision of a researcher, which naturally limited the timespan over which observations were made. Here, we introduce a new and unsupervised method to continuously record the EODs of weakly electric fish. Our approach is based on the deployment of autonomously operating logging devices. In comparison with the previously used electrode arrays, observations from individual loggers lack the spatial resolution that is necessary to track animals and document detailed behavioral interactions. Nevertheless, there are certain benefits to this approach. Distribution of individual loggers allowed us to sample from different habitats and cover a larger area than would have been possible using an electrode array, and it enabled us to make observations over longer timespans than previously possible. The low price per unit (ca. 70 €) makes this technology accessible and reduces the financial risk of loss of equipment in the field. Open source microcontroller technology, such as the Teensy, and the Arduino programming language are used by a large community of scientists and non-scientists. These features make the EOD logger a promising and open tool for studies that focus on longer-term temporal patterns, or that are conducted in challenging environments that are difficult to access, such as swamps and lakes. For future applications, it is conceivable that the recording program can be adapted to allow the connection of multiple EOD loggers to record with higher spatial resolution from areas of interest.

CONCLUSION

This study shows nocturnal behavior of two mormyrid fishes that persist in a habitat with extreme nocturnal hypoxia. Activity increases corresponded directly to ambient light levels indicating that light is an important environmental cue and/or zeitgeber for endogenous clocks. Compared to laboratory observations, nocturnal activity increases were less pronounced in the field, which is possibly due to lower nocturnal water temperatures, hypoxia, and a higher environmental complexity that fosters a higher diurnal activity level. Habitat use shifted between a strong preference for complex habitats during the day to increased activity in open and unprotected areas during the night, when DO concentrations are lowest. Co-occurrences suggest that social

interactions take place in both species mostly during the active phase at night, and in the case of *M. victoriae* mostly in the open areas of the habitat, although further investigation is needed for a detailed description of the nocturnal social behavior of the study species. Given their preference for structurally complex habitats, freshwater ecosystems with dense vegetation are likely to play an important role in the ecology of the study species.

DATA AVAILABILITY STATEMENT

The original data presented in the study are publicly available at: doi: 10.6084/m9.figshare.19526155.v3.

ETHICS STATEMENT

The animal study was reviewed and approved by Landesamt für Gesundheit und Soziales, Berlin, Germany.

AUTHOR CONTRIBUTIONS

All authors participated in the design of this study. SM developed the EOD logger, performed the field work and laboratory experiments with *P. degeni*, and data analyses. FO conducted the laboratory experiments with *M. victoriae*. SM drafted the manuscript and all authors took part in its revision.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.870043/full#supplementary-material>

REFERENCES

- Ackerly, K. L., Krahe, R., Sanford, C. P., and Chapman, L. J. (2018). Effects of hypoxia on swimming and sensing in a weakly electric fish. *J. Exp. Biol.* 2018:221. doi: 10.1242/jeb.172130
- Adamovich, Y., Ladeux, B., Golik, M., Koeners, M. P., and Asher, G. (2017). Rhythmic oxygen levels reset circadian clocks through HIF1 α . *Cell Metab.* 25, 93–101. doi: 10.1016/j.cmet.2016.09.014
- Adebisi, A. A. (1981). The physico-chemical hydrology of a tropical seasonal river - upper Ogun river. *Hydrobiologia* 79, 157–165. doi: 10.1007/bf00006123
- Ardanaz, J. L., Silva, A., and Macadar, O. (2001). Temperature sensitivity of the electric organ discharge waveform in *Gymnotus carapo*. *J. Comp. Physiol. A* 187, 853–864. doi: 10.1007/s00359-001-0256-8
- Arrington, D. A., and Winemiller, K. O. (2003). Diel changeover in sandbank fish assemblages in a neotropical floodplain river. *J. Fish Biol.* 63, 442–459. doi: 10.1046/j.1095-8649.2003.00167.x
- Aschoff, J. (1960). Exogenous and endogenous components in circadian rhythms. *Cold Spring Harb. Symp. Quant. Biol.* 25, 11–28. doi: 10.1101/sqb.1960.025.01.004
- Bässler, G., Hilbig, R., and Rahmann, H. (1979). Untersuchungen zur circadianen Rhythmik der elektrischen und motorischen Aktivität von *Gnathonemus petersii* (Mormyridae, Pisces). *Z. Tierpsychol.* 49, 156–163. doi: 10.1111/j.1439-0310.1979.tb00284.x
- Baumann, H., Wallace, R. B., Tagliaferri, T., and Gobler, C. J. (2015). Large natural pH, CO₂ and O₂ fluctuations in a temperate tidal salt marsh on diel, seasonal, and interannual time scales. *Estuaries Coasts* 38, 220–231. doi: 10.1007/s12237-014-9800-y
- Beamish, F. W. H. (1964). Respiration of fishes with special emphasis on standard oxygen consumption: II. Influence of weight and temperature on respiration of several species. *Can. J. Zool.* 42, 177–188. doi: 10.1139/z64-016
- Benda, J. (2020). “The Physics of Electrosensory Worlds,” in *The Senses: A Comprehensive Reference*, ed. B. Fritzsche (Cambridge, MA: Academic Press), 228–254. doi: 10.1016/b978-0-12-805408-6.00016-6
- Boujard, T., and Leatherland, J. F. (1992). Circadian rhythms and feeding time in fishes. *Environ. Biol. Fish.* 35, 109–131. doi: 10.1007/bf00002186
- Campos-Candela, A., Palmer, M., Balle, S., and Alós, J. (2018). A camera-based method for estimating absolute density in animals displaying home range behaviour. *J. Anim. Ecol.* 87, 825–837. doi: 10.1111/1365-2656.12787
- Carlson, B. A. (2002). Electric signaling behavior and the mechanisms of electric organ discharge production in mormyrid fish. *J. Physiol. Paris* 96, 405–419. doi: 10.1016/S0928-4257(03)00019-6
- Carlson, B. A. (2016). Differences in electrosensory anatomy and social behavior in an area of sympatry between two species of mormyrid electric fishes. *J. Exp. Biol.* 219, 31–43. doi: 10.1242/jeb.127720
- Carlson, B. A., and Hopkins, C. D. (2004). Stereotyped temporal patterns in electrical communication. *Anim. Behav.* 68, 867–878. doi: 10.1016/j.anbehav.2003.10.031
- Chapman, L. J., and Chapman, C. A. (1998). Hypoxia tolerance of the mormyrid *Petrocephalus catostoma*. implications for persistence in swamp refugia. *Copeia* 1998:762. doi: 10.2307/1447812
- Chapman, L. J., and Hulén, K. G. (2001). Implications of hypoxia for the brain size and gill morphology of mormyrid fishes. *J. Zool.* 254, 461–472. doi: 10.1017/s0952836901000966
- Chapman, L. J., Chapman, C. A., Ogutu-Ohwayo, R., Chandler, M., Kaufman, L., and Keiter, A. E. (1996b). Refugia for endangered fishes from an introduced predator in Lake Nabugabo, Uganda. *Conserv. Biol.* 10, 554–561. doi: 10.1046/j.1523-1739.1996.10020554.x
- Chapman, L. J., Chapman, C. A., and Chandler, M. (1996a). Wetland ecotones as refugia for endangered fishes. *Biol. Conserv.* 78, 263–270. doi: 10.1016/s0006-3207(96)00030-4
- Chapman, L. J., Chapman, C. A., Nordlie, F. G., and Rosenberger, A. E. (2002). Physiological refugia: swamps, hypoxia tolerance and maintenance of fish diversity in the Lake Victoria region. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* 133, 421–437. doi: 10.1016/s1095-6433(02)00195-2
- Chapman, L. J., Chapman, C. A., Schofield, P. J., Olowo, J. P., Kaufman, L., Seehausen, O., et al. (2003). Fish faunal resurgence in Lake Nabugabo, East Africa. *Conserv. Biol.* 17, 500–511. doi: 10.1046/j.1523-1739.2003.01519.x
- Chrétien, E., and Chapman, L. J. (2016). Habitat heterogeneity facilitates coexistence of native fishes with an introduced predator. the resilience of a fish community 5 decades after the introduction of Nile perch. *Biol. Invasions* 18, 3449–3464. doi: 10.1007/s10530-016-1235-x
- Clarke, S. B., Chapman, L. J., and Krahe, R. (2020). The effect of normoxia exposure on hypoxia tolerance and sensory sampling in a swamp-dwelling mormyrid fish. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* 2020:240. doi: 10.1016/j.cbpa.2019.110586
- Cobert, S. J. (1984). *Environmental control of rhythmic behavior in the weak-electric fish, Gnathonemus petersii (Mormyridae)*. Ph.D. thesis, New York, NY.
- Crampton, W. G. R. (1996). Gymnotiform fish. An important component of Amazonian floodplain fish communities. *J. Fish Biol.* 48, 298–301. doi: 10.1006/jfbi.1996.0029
- Crampton, W. G. R. (1998). Effects of anoxia on the distribution, respiratory strategies and electric signal diversity of gymnotiform fishes. *J. Fish Biol.* 53, 307–330. doi: 10.1111/j.1095-8649.1998.tb01034.x
- Crampton, W. G. R. (2019). Electroreception, electrogenesis and electric signal evolution. *J. Fish Biol.* 95, 92–134. doi: 10.1111/jfb.13922
- Dunlap, K. D., Smith, G. T., and Yekta, A. (2000). Temperature dependence of electrocommunication signals and their underlying neural rhythms in the weakly electric fish. *Apteronotus leptorhynchus*. *Brain Behav. Evol.* 55, 152–162. doi: 10.1159/000006649
- Egg, M., Köblitz, L., Hirayama, J., Schwerte, T., Folterbauer, C., Kurz, A., et al. (2013). Linking oxygen to time: the bidirectional interaction between the hypoxic signaling pathway and the circadian clock. *Chronobiol. Int.* 30, 510–529. doi: 10.3109/07420528.2012.754447
- Emde, G. (1999). Active electrolocation of objects in weakly electric fish. *J. Exp. Biol.* 202, 1205–1215. doi: 10.1242/jeb.202.10.1205
- Emde, G., and Bleckmann, H. (1998). Finding food: senses involved in foraging for insect larvae in the electric fish *Gnathonemus petersii*. *J. Exp. Biol.* 201(Pt 7), 969–980. doi: 10.1242/jeb.201.7.969
- Follana-Berná, G., Palmer, M., Lekanda-Guarrotxena, A., Grau, A., and Arechavala-Lopez, P. (2020). Fish density estimation using unbaited cameras: accounting for environmental-dependent detectability. *J. Exp. Mar. Biol. Ecol.* 527:151376. doi: 10.1016/j.jembe.2020.151376
- Franchina, C. R., and Stoddard, P. K. (1998). Plasticity of the electric organ discharge waveform of the electric fish *Brachyhyopomus pinnicaudatus*. I. Quantification of day-night changes. *J. Comp. Physiol. A* 183, 759–768. doi: 10.1007/s003590050299
- Franchina, C. R., Salazar, V. L., Volmar, C. H., and Stoddard, P. K. (2001). Plasticity of the electric organ discharge waveform of male *Brachyhyopomus pinnicaudatus*. II. Social effects. *J. Comp. Physiol. A* 187, 45–52. doi: 10.1007/s003590000176
- Frehse, F. D. A., Weyl, O. L. F., and Vitule, J. R. S. (2020). Comparison of visual census and underwater video for fish sampling in Neotropical reservoirs. *Environ. Biol. Fish.* 103, 1269–1277. doi: 10.1007/s10641-020-01021-3
- Frehse, F. D. A., Weyl, O. L. F., and Vitule, J. R. S. (2021). Differential use of artificial habitats by native and non-native fish species in Neotropical reservoirs. *Hydrobiologia* 848, 2355–2367. doi: 10.1007/s10750-021-04564-3
- Friedman, M. A., and Hopkins, C. D. (1996). Tracking individual mormyrid electric fish in the field using electric organ discharge waveforms. *Anim. Behav.* 51, 391–407. doi: 10.1242/jeb.226340
- Frøland Steindal, I. A., and Whitmore, D. (2019). Circadian clocks in fish-what have we learned so far? *Biology* 2019:8. doi: 10.3390/biology8010017
- Greenbank, J. (1945). Limnological conditions in ice-covered lakes, especially as related to winter-kill of fish. *Ecol. Monogr.* 15, 343–392. doi: 10.2307/1948427
- Greenwood, P. H. (1965). *The cichlid fishes of Lake Nabugabo, Uganda*. London: British Museum.
- Häfker, N. S., and Tessmar-Raible, K. (2020). Rhythms of behavior: are the times changin'? *Curr. Opin. Neurobiol.* 60, 55–66. doi: 10.1016/j.conb.2019.10.005
- Hamilton, S. K. (2010). Biogeochemical implications of climate change for tropical rivers and floodplains. *Hydrobiologia* 657, 19–35. doi: 10.1007/s10750-009-0086-1
- Hammerschlag, N., Heithaus, and Serafy, J. E. (2010). Influence of predation risk and food supply on nocturnal fish foraging distributions along a mangrove-seagrass ecotone. *Mar. Ecol. Prog. Ser.* 414, 223–235. doi: 10.3354/meps08731

- Harder, W., Schief, A., and Uhlemann, H. (1964). Zur Funktion des elektrischen Organs von *Gnathonemus petersii* (Gthr. 1862) (Mormyriiformes, Teleostei). *Z. vergl. Physiologie* 48, 302–331. doi: 10.1007/bf00339459
- Henninger, J., Krahe, R., Kirschbaum, F., Grewe, J., and Benda, J. (2018). Statistics of natural communication signals observed in the wild identify important yet neglected stimulus regimes in weakly electric fish. *J. Neurosci.* 38, 5456–5465. doi: 10.1523/JNEUROSCI.0350-18.2018
- Henninger, J., Krahe, R., Sinz, F., and Benda, J. (2020). Tracking activity patterns of a multispecies community of gymnotiform weakly electric fish in their Neotropical habitat without tagging. *J. Exp. Biol.* 2020:223. doi: 10.1242/jeb.206342
- Hobson, E. S. (1973). Diel feeding migrations in tropical reef fishes. *Helgoländer wiss. Meeresunters* 24, 361–370. doi: 10.1007/bf01609526
- Hopkins, C. D. (1980). Evolution of electric communication channels of mormyrids. *Behav. Ecol. Sociobiol.* 7, 1–13. doi: 10.1007/bf00302513
- Hopkins, C. D., and Bass, A. H. (1981). Temporal coding of species recognition signals in an electric fish. *Science* 212, 85–87. doi: 10.1126/science.7209524
- Hurd, M., DeBruyne, J., Straume, M., and Cahill, G. M. (1998). Circadian rhythms of locomotor activity in zebrafish. *Physiol. Behav.* 65, 465–472. doi: 10.1016/s0031-9384(98)00183-8
- Hut, R. A., Paolucci, S., Dor, R., Kyriacou, C. P., and Daan, S. (2013). Latitudinal clines: an evolutionary view on biological rhythms. *Proc. R. Soc. B* 280:20130433. doi: 10.1098/rspb.2013.0433
- Ibbotson, A. T., Beaumont, W. R. C., Pinder, A., Welton, S., and Ladle, M. (2006). Diel migration patterns of Atlantic salmon smolts with particular reference to the absence of crepuscular migration. *Ecol. Freshw. Fish* 15, 544–551. doi: 10.1111/j.1600-0633.2006.0194.x
- Kannan, V., and Job, S. V. (1980). Diurnal depth-wise and seasonal changes of physico-chemical factors in Sathiar reservoir. *Hydrobiologia* 70, 103–117. doi: 10.1007/bf00015496
- Kaufman, L., and Ochumba, P. (1993). Evolutionary and conservation biology of cichlid fishes as revealed by faunal remnants in northern Lake Victoria. *Conserv. Biol.* 7, 719–730. doi: 10.1046/j.1523-1739.1993.07030719.x
- Kirschbaum, F. (1995). “Reproduction and development in mormyrid and gymnotiform fishes,” in *Electric fishes: history and behavior*, ed. P. Moller (London: Chapman and Hall), 267–301.
- Kirschbaum, F., and Schugardt, C. (2002). Reproductive strategies and developmental aspects in mormyrid and gymnotiform fishes. *J. Physiol.* 96, 557–566. doi: 10.1016/S0928-4257(03)00011-1
- Kramer, D. L., Manley, D., and Bourgeois, R. (1983). The effect of respiratory mode and oxygen concentration on the risk of aerial predation in fishes. *Can. J. Zool.* 61, 653–665. doi: 10.1139/z83-087
- Kruger, E. J. (1973). Autumn feeding cycle of the bull-dog fish, *Gnathonemus macrolepidotus* (Pisces, Mormyridae). *Afr. Zool.* 8, 25–34. doi: 10.1080/00445096.1973.11447463
- Lewis, J. E., Gilmour, K. M., Moorhead, M. J., Perry, S. F., and Markham, M. R. (2014). Action potential energetics at the organismal level reveal a trade-off in efficiency at high firing rates. *J. Neurosci.* 34, 197–201. doi: 10.1523/JNEUROSCI.3180-13.2014
- Lewis, W. M. (1970). Morphological adaptations of cyprinodontoids for inhabiting oxygen deficient waters. *Copeia* 1970, 319–326. doi: 10.2307/1441653
- Lissmann, H. W. (1951). Continuous electrical signals from the tail of a fish. *Gymnarc. Niloticus Cuv.* 167, 201–202. doi: 10.1038/167201a0
- Lissmann, H. W. (1958). On the function and evolution of electric organs in fish. *J. Exp. Biol.* 35, 156–191. doi: 10.1242/jeb.35.1.156
- Lissmann, H. W. (1961). “Ecological studies on gymnotids,” in *Bioelectrogenesis. A comparative survey of its mechanisms with particular emphasis on electric fishes*, eds C. Chagas and A. P. de Carvalho (Amsterdam: Elsevier), 215–226.
- Lissmann, H. W., and Machin, K. E. (1958). The mechanism of object location in *Gymnarchus niloticus* and similar fish. *J. Exp. Biol.* 35, 451–486. doi: 10.1242/jeb.35.2.451
- Lissmann, H. W., and Schwassmann, H. O. (1965). Activity rhythm of an electric fish, *Gymnorhamphichthys hypostomus*, Ellis. *J. Comp. Physiol. A* 51, 153–171. doi: 10.1007/bf00299291
- Lundberg, J. G., Lewis, W. M., Saunders, J. F., and Mago-Leccia, F. (1987). A major food web component in the orinoco river channel: evidence from planktivorous electric fishes. *Science* 237, 81–83. doi: 10.1126/science.237.4810.81
- Madhav, M. S., Jayakumar, R. P., Demir, A., Stamper, S. A., Fortune, E. S., and Cowan, N. J. (2018). High-resolution behavioral mapping of electric fishes in Amazonian habitats. *Sci. Rep.* 8:5830. doi: 10.1038/s41598-018-24035-5
- Markham, M. R., Ban, Y., McCauley, A. G., and Maltby, R. (2016). Energetics of sensing and communication in electric fish: a blessing and a curse in the anthropocene? *Integr. Comp. Biol.* 56, 889–900. doi: 10.1093/icb/icw104
- Markham, M. R., McAnelly, M. L., Stoddard, P. K., and Zakon, H. H. (2009). Circadian and social cues regulate ion channel trafficking. *PLoS Biol.* 7:e1000203. doi: 10.1371/journal.pbio.1000203
- Migliaro, A., and Silva, A. C. (2016). Melatonin regulates daily variations in electric behavior arousal in two species of weakly electric fish with different social structures. *Brain Behav. Evol.* 87, 232–241. doi: 10.1159/000445494
- Migliaro, A., Moreno, V., Marchal, P., and Silva, A. C. (2018). Daily changes in the electric behavior of weakly electric fish naturally persist in constant darkness and are socially synchronized. *Biol. Open* 2018:7. doi: 10.1242/bio.036319
- Moller, P. (1970). ‘Communication’ in weakly electric fish, *Gnathonemus niger* (Mormyridae) I. Variation of electric organ discharge (EOD) frequency elicited by controlled electric stimuli. *Anim. Behav.* 18, 768–786. doi: 10.1016/0003-3472(70)90026-6
- Moller, P. (1995). *Electric fishes: history and behavior*. London: Chapman & Hall.
- Moller, P., and Bauer, R. (1973). ‘Communication’ in weakly electric fish, *Gnathonemus petersii* (Mormyridae) II. Interaction of electric organ discharge activities of two fish. *Anim. Behav.* 21, 501–512. doi: 10.1016/s0003-3472(73)80010-7
- Moller, P., Serrier, J., and Bowling, D. (1989). Electric Organ Discharge Displays during Social Encounter in the Weakly Electric Fish *Brienomyrus niger* L. (Mormyridae). *Ethology* 82, 177–191. doi: 10.1111/j.1439-0310.1989.tb00498.x
- Moller, P., Serrier, J., Belbenoit, P., and Push, S. (1979). Notes on ethology and ecology of the Swashi River mormyrids (Lake Kainji, Nigeria). *Behav. Ecol. Sociobiol.* 4, 357–368. doi: 10.1007/bf00303242
- Mönck, H. J., Jorg, A., Falkenhausen, T. V., Tanke, J., Wild, B., Dormagen, D., et al. (2018). BioTracker: an open-source computer vision framework for visual animal tracking. *arXiv* 1803:07985v1.
- Moulton, T. L., Chapman, L. J., and Krahe, R. (2020). Effects of hypoxia on aerobic metabolism and active electrosensory acquisition in the African weakly electric fish *Marcusenius victoriae*. *J. Fish Biol.* 96, 496–505. doi: 10.1111/jfb.14234
- Nagelkerken, I., Dorenbosch, M., Verberk, W., La Cocheret, de Morinière, E., and van der Velde, G. (2000). Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. *Mar. Ecol. Prog. Ser.* 194, 55–64. doi: 10.3354/meps194055
- Naylor, E. (2010). *Chronobiology of Marine Organisms*. Cambridge, MA: Cambridge University Press.
- Neilson, J. D., and Perry, R. I. (1990). *Diel Vertical Migrations of Marine Fishes: an Obligate or Facultative Process? in Advances in Marine Biology*, Vol. 26. Amsterdam: Elsevier, 115–168.
- Nyboer, E. A., and Chapman, L. J. (2013). Movement and home range of introduced Nile perch (*Lates niloticus*) in Lake Nabugabo, Uganda: implications for ecological divergence and fisheries management. *Fish. Res.* 137, 18–29. doi: 10.1016/j.fishres.2012.08.003
- Ogutu-Ohwayo, R. (1993). The effects of predation by Nile perch, *Lates niloticus* L., on the fish of Lake Nabugabo, with suggestions for conservation of endangered endemic cichlids. *Conserv. Biol.* 7, 701–711. doi: 10.1046/j.1523-1739.1993.07030701.x
- Pelster, B., and Egg, M. (2018). Hypoxia-inducible transcription factors in fish: expression, function and interconnection with the circadian clock. *J. Exp. Biol.* 2018:221. doi: 10.1242/jeb.163709
- Pollock, M. S., Clarke, L. M. J., and Dubé, M. G. (2007). The effects of hypoxia on fishes. from ecological relevance to physiological effects. *Environ. Rev.* 15, 1–14. doi: 10.1139/a06-006
- Pringle, R. M. (2005). The origins of the Nile perch in Lake Victoria. *Bioscience* 55, 780–787. doi: 10.1641/0006-3568(2005)055[0780:tootnp]2.0.co;2
- Reardon, E. E., and Chapman, L. J. (2008). Reproductive seasonality in a swamp-locked African cichlid. *Ecol. Freshw. Fish* 17, 20–29. doi: 10.1111/j.1600-0633.2007.00251.x
- Reebs, S. G. (1994). The anticipation of night by fry-retrieving convict cichlids. *Anim. Behav.* 48, 89–95. doi: 10.1006/anbe.1994.1214

- Reebs, S. G. (2002). Plasticity of diel and circadian activity rhythms in fishes. *Rev. Fish Biol. Fish.* 12, 349–371. doi: 10.1023/A:1025371804611
- Rooker, J. R., and Dennis, G. D. (1991). Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. *Bull. Mar. Sci.* 49, 684–698.
- Rowland, W. J. (1999). Studying visual cues in fish behavior: A review of ethological techniques. *Environ. Biol. Fish.* 56, 285–305. doi: 10.1023/a:1007517720723
- Saint-Paul, U., and Soares, G. M. (1987). Diurnal distribution and behavioral responses of fishes to extreme hypoxia in an Amazon floodplain lake. *Environ. Biol. Fish.* 20, 91–104. doi: 10.1007/bf00005289
- Salazar, V. L., and Stoddard, P. K. (2008). Sex differences in energetic costs explain sexual dimorphism in the circadian rhythm modulation of the electrocommunication signal of the gymnotiform fish *Brachyhyopomus pinnicaudatus*. *J. Exp. Biol.* 211, 1012–1020. doi: 10.1242/jeb.014795
- Salazar, V. L., Krahe, R., and Lewis, J. E. (2013). The energetics of electric organ discharge generation in gymnotiform weakly electric fish. *J. Exp. Biol.* 216, 2459–2468. doi: 10.1242/jeb.082735
- Sánchez-Vázquez, F. J., Madrid, J. A., and Zamora, S. (1995). Circadian rhythms of feeding activity in sea bass, *Dicentrarchus labrax* L.: dual phasing capacity of diel demand-feeding pattern. *J. Biol. Rhythms* 10, 256–266. doi: 10.1177/074873049501000308
- Sandbichler, A. M., Jansen, B., Peer, B. A., Paulitsch, M., Pelster, B., and Egg, M. (2018). Metabolic plasticity enables circadian adaptation to acute hypoxia in zebrafish cells. *Cell. Physiol. Biochem.* 46, 1159–1174. doi: 10.1159/000489058
- Savitzky, A., and Golay, M. J. E. (1964). Smoothing and differentiation of data by simplified least squares procedures. *Anal. Chem.* 36, 1627–1639. doi: 10.1021/ac60214a047
- Scheffel, A., and Kramer, B. (1997). Electrocommunication and social behaviour in *Marcusenius senegalensis* (Mormyridae, Teleostei). *Ethology* 103, 404–420. doi: 10.1111/j.1439-0310.1997.tb00156.x
- Schödel, J., Oikonomopoulos, S., Ragoussis, J., Pugh, C. W., Ratcliffe, P. J., and Mole, D. R. (2011). High-resolution genome-wide mapping of HIF-binding sites by ChIP-seq. *Blood* 117, e207–e217. doi: 10.1182/blood-2010-10-314427
- Semesi, I. S., Beer, S., and Björk, M. (2009). Seagrass photosynthesis controls rates of calcification and photosynthesis of calcareous macroalgae in a tropical seagrass meadow. *Mar. Ecol. Prog. Ser.* 382, 41–47. doi: 10.3354/meps07973
- Sikkel, P. C., Welicky, R. L., Artim, J. M., McCammon, A. M., Sellers, J. C., Coile, A. M., et al. (2017). Nocturnal migration reduces exposure to micropredation in a coral reef fish. *Bull. Mar. Sci.* 93, 475–489. doi: 10.5343/bms.2016.1021
- Silva, A. C., Perrone, R., and Macadar, O. (2007). Environmental, seasonal, and social modulations of basal activity in a weakly electric fish. *Physiol. Behav.* 90, 525–536. doi: 10.1016/j.physbeh.2006.11.003
- Stager, J. C., Westwood, J., Grzesik, D., and Cumming, B. F. (2005). A 5500-year environmental history of Lake Nabugabo, Uganda. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 218, 347–354. doi: 10.1016/j.palaeo.2004.12.025
- Stoddard, P. K., Markham, M. R., Salazar, V. L., and Allee, S. (2007). Circadian rhythms in electric waveform structure and rate in the electric fish *Brachyhyopomus pinnicaudatus*. *Physiol. Behav.* 90, 11–20. doi: 10.1016/j.physbeh.2006.08.013
- Sukhum, K. V., Freiler, M. K., Wang, R., and Carlson, B. A. (2016). The costs of a big brain. Extreme encephalization results in higher energetic demand and reduced hypoxia tolerance in weakly electric African fishes. *Proc. R. Soc. B* 2016:283. doi: 10.1098/rspb.2016.2157
- Tabata, M., Minh-Nyo, M., Niwa, H., and Oguri, M. (1989). Circadian rhythm of locomotor activity in a teleost, *Silurus asotus*. *Zool. Sci.* 6, 367–375.
- Talling, J. F. (1957). Diurnal changes of stratification and photosynthesis in some tropical African waters. *Proc. R. Soc. B* 147, 57–83. doi: 10.1098/rspb.1957.0036
- Toerring, M. J., and Serrier, J. (1978). Influence of water temperature on the electric organ discharge (EOD) of the weakly electric fish *Marcusenius cyprinoides* (Mormyridae). *J. Exp. Biol.* 74, 133–150. doi: 10.1242/jeb.74.1.133
- Townsend, S. A. (1999). The seasonal pattern of dissolved oxygen, and hypolimnetic deoxygenation, in two tropical Australian reservoirs. *Lakes Reserv.* 4, 41–53. doi: 10.1046/j.1440-1770.1999.00077.x
- Trewavas, E. (1933). Scientific results of the Cambridge Expedition to the East African Lakes, 1930-1.-11. The cichlid fishes. *Zool. J. Linn. Soc.* 38, 309–341. doi: 10.1111/j.1096-3642.1933.tb00062.x
- Ultsch, G. R., Boschung, H., and Ross, M. J. (1978). Metabolism, critical oxygen tension, and habitat selection in darters (*Etheostoma*). *Ecology* 59, 99–107. doi: 10.2307/1936635
- Vanderpham, J. P., Nakagawa, S., and Closs, G. P. (2012). Diel variation in use of cover and feeding activity of a benthic freshwater fish in response to olfactory cues of a diurnal predator. *Environ. Biol. Fish.* 93, 547–556. doi: 10.1007/s10641-011-9949-1
- Volpato, G. L., and Trajano, E. (2005). *Biological Rhythm in The Physiology of Tropical Fishes*. Cambridge, MA: Academic Press, 101–153.
- Wenger, R. H., Stiehl, D. P., and Camenisch, G. (2005). Integration of oxygen signaling at the consensus HRE. *Sci.* 2005:re12. doi: 10.1126/stke.3062005re12
- Whitmore, D., Foulkes, N. S., and Sassone-Corsi, P. (2000). Light acts directly on organs and cells in culture to set the vertebrate circadian clock. *Nature* 404, 87–91. doi: 10.1038/35003589
- Wulund, L., and Reddy, A. B. (2015). A brief history of circadian time: The emergence of redox oscillations as a novel component of biological rhythms. *Perspect. Sci.* 6, 27–37. doi: 10.1016/j.pisc.2015.08.002

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